

A GENERIC REVISION OF THE STYLASTERINA (COELENTERATA: HYDROZOA).

PART 1. DESCRIPTION OF THE GENERA

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ABSTRACT

Prior to a phylogenetic analysis of the Stylasterina, the 23 genera and one subgenus in the order are redescribed with special emphasis on scanning electron microscopy of the skeleton, histology of soft parts, and variation within each genus. Two new genera are described. The type-species of each genus is also redescribed and figured by scanning electron micrographs. Tissue of 21 of the 23 Recent genera and subgenera was examined by histological serial sections; 18 of these 21 were type-species of genera. The first three-dimensional (SEM) photographs of stylasterine nematocysts are provided. Much of the terminology used to describe stylasterines is reviewed and some new terms introduced.

A critical checklist of all stylasterine taxa is given, which includes 23 genera, 1 subgenus, 184 valid species, 7 subspecies, 11 formae or facies, and 42 synonyms. Numerous new synonyms and new combinations are made in this checklist, many of the latter caused by the synonymy of *Allopورا* with *Stylaster*.

This is the first of a two-part study to redefine and phylogenetically analyze the genera of Stylasterina. Here, the 23 genera and 1 subgenus are redescribed based on the traditionally used gross skeletal characteristics and augmented with scanning electron microscopy of the skeleton and histological examination of the soft parts. The type-species of each genus is given special attention in describing the genera; however, as many species as possible were examined in an attempt to place each species in the correct genus and to better define the variation within each genus. The order of the subfamilies and the genera within each subfamily was determined by their degree of morphological complexity: the simplest, least modified genera first; the complex, most highly modified genera last. Character state series used to rank the genera are briefly discussed by Cairns (in press); however, a thorough analysis of the character states, their polarity, and a phylogenetic analysis of the genera will form the basis of the second paper of this study.

MATERIAL AND METHODS

Material.—Of the 244 nominal taxa of Stylasterina (Table 1: species, subspecies, formae, synonyms but not nomina nuda), the type-specimens of 54 were examined from the United States National Museum (USNM) and an additional 67 were examined on loan from other museums, for a total of 121, or 50% of all taxa. Additional nontype specimens were examined from the USNM, and of the 202 valid taxa (not including synonyms and nomina nuda), I have examined 146 (type and/or nontype), representing 72% of all taxa of Stylasterina. Specimens were borrowed from: British Museum (Natural History), London (BM); Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); Museum of Comparative Zoology, Harvard, Cambridge (MCZ); Zoologisch Museum, Amsterdam (ZMA); Zoologisk Museum, Copenhagen; Geologisk Museum, Copenhagen; Zoologisches Museum, Berlin; and Naturhistoriska Riksmuseet, Stockholm.

Methods.—Scanning electron microscopy (SEM) is a particularly good technique for the study and illustration of small stylasterine structures, such as gastro- and dactylostyles and coenosteal texture. Ordinarily a natural or induced fracture revealed these structures, but if material was scarce and the styles delicate or well protected (longitudinally instead of radially disposed), I used an ultra-high-speed precision air grinder (Dentsply 300 KS, #55001, 55006) with a 1-mm-diameter burr for removal of excess calcium carbonate to reveal the structure. Most of the SEM photomicrographs were made with

Table 1. Checklist of the nominal species of Stylasterina. The arrangement of genera within subfamilies was determined by increasing morphological complexity, following, in general, the character state series proposed by Cairns (In press). The order of species within genera is geographic, those from the Indian Ocean first, proceeding eastward, and concluding with the Antarctic. The type-species of each genus is indicated by an asterisk (*); fossil species are indicated by crosses (+); junior synonyms are indented and preceded with an equals sign; and species of uncertain generic placement are preceded with a question mark. Currently there are 23 genera, 1 subgenus, 184 valid species, 7 subspecies, 11 formae or facies, 4 nomina nuda, 4 unnamed "species," and 42 junior synonyms of Stylasterina

Subfamily Errininae Hickson, 1912	1879) n. comb.
* <u>Lepidopora glabra</u> Pourtalès, 1867	* <u>Errinopsis reticulum</u> Broch, 1951
<u>L. decipiens</u> Boschma, 1964	<u>E. fenestrata</u> Cairns, 1983
<u>L. carinata</u> (Portalès, 1867)	<u>Errina novaezealandiae</u> Hickson, 1912
<u>L. hicksoni</u> Boschma, 1963	facies <u>ramosa</u> Hickson, 1912
<u>L. diffusa</u> Boschma, 1963	facies <u>benhami</u> Hickson, 1912
<u>L. sarmentosa</u> Boschma, 1968	facies <u>dendeyi</u> Hickson, 1912
<u>L. granulosa</u> (Cairns, 1983)	facies <u>cooki</u> Hickson, 1912
<u>L. acrolophos</u> Cairns, 1983	<u>E. rubra</u> Broch, 1942
<u>Sporadopora mortenseni</u> Broch, 1942	<u>E. cruenta</u> Boschma, 1968
+ <u>S. marginata</u> Tenison-Woods, 1880	? <u>E. macrogastra</u> Marenzeller, 1904
?+ <u>S. faxensis</u> Nielsen, 1919	<u>E. cochleata</u> Pourtalès, 1867
* <u>S. dichotoma</u> (Moseley, 1877)	<u>E. dabneyi</u> Pourtalès, 1871
<u>Pliobothrus spinosa</u> (Hickson & England, 1905)	= <u>E. amoena</u> Boschma, 1956
* <u>P. symmetricus</u> Pourtalès, 1868	* <u>E. aspera</u> (Linnaeus, 1767)
<u>P. tubulatus</u> (Portalès, 1867)	<u>E. a. mascarina</u> Boschma, 1965
?+ <u>P. dispergens</u> Nielsen, 1919	<u>E. atlantica</u> Hickson, 1912
?+ <u>P. laevis</u> Nielsen, 1919	* <u>E. irregularis</u> (Nielsen, 1919)
* <u>Cheiloporidion pulvinatum</u> Cairns, 1983	<u>E. capensis</u> Hickson, 1912
<u>Lepidotheca tenuistylus</u> (Broch, 1942) n. comb.	<u>E. antarctica</u> (Gray, 1872)
<u>L. cervicornis</u> (Broch, 1942) n. comb.	= <u>E. moseleyi</u> Ridley, 1881
<u>L. horrida</u> (Hickson & England, 1905) n. comb.	= <u>E. spongiosa</u> Broch, 1942
<u>L. ramosa</u> (Hickson & England, 1905) n. comb.	<u>E. fissurata</u> Gray, 1872
<u>L. hachijoensis</u> (Eguchi, 1968) n. comb.	<u>E. gracilis</u> Marenzeller, 1903
<u>L. japonica</u> (Eguchi, 1968) n. comb.	<u>E. kerguelensis</u> Broch, 1942
* <u>L. fascicularis</u> (Cairns, 1983) n. comb.	<u>E. laterorifa</u> Eguchi, 1964
* <u>Phalangopora regularis</u> Kirkpatrick, 1887	= <u>E. carnea</u> Boschma, 1964
= <u>Pliobothrus seriatus</u> Broch, 1942	<u>E. boschmai</u> Cairns, 1983
* <u>Inferiolabiata labiata</u> (Moseley, 1879)	<u>E. cheilopora</u> Cairns, 1983
<u>I. lowei</u> Cairns, 1983	<u>Errinopora stylifera</u> (Broch, 1935)
* <u>Paraerrina decipiens</u> Broch, 1942	= <u>E. intervacans</u> Naumov, 1960
? <u>P. spp.</u> Squires, 1962	? <u>E. porifera</u> (Naumov, 1960)
* <u>Stellapora echinata</u> (Moseley, 1879)	<u>E. latifundata</u> Naumov, 1960
	<u>E. nanneca</u> Fisher, 1938
	<u>E. zarhyncha</u> Fisher, 1938
	* <u>E. pourtalesii</u> (Dall, 1884)
	?+ <u>E. lobata</u> (Nielsen, 1919)
	<u>E. cestoporina</u> Cairns, 1983
	? <u>E. cyclopora</u> (Cairns, 1983)
	* <u>Gyropora africana</u> Boschma, 1960
	Subfamily Adeloporinae Cairns, 1982
	* <u>Adelopora pseudothyron</u> Cairns, 1982
	Subfamily Distichoporinae Stechow, 1921

Table 1. Continued

<u>Distichopora</u> (D.) <u>profunda</u> Hickson & England, 1909	1968) n. comb.
D. <u>providentiae</u> (Hickson & England, 1909)	S. <u>solidus</u> Broch, 1935
*D. <u>violacea</u> (Pallas, 1766)	S. <u>boreopacificus</u> Broch, 1932
=D. <u>cinnabarina</u> Nardo, 1844	S. <u>incrassatus</u> (Eguchi, 1941)
?=D. <u>fulvacea</u> Michelin, 1862	S. <u>brochi</u> (Fisher, 1938) n. comb.
?=D. <u>rosea</u> Kent, 1871	S. <u>moseleyanus</u> (Fisher, 1938) n. comb.
=D. <u>fisheri</u> Broch, 1942	S. m. forma <u>leptostylus</u> (Fisher, 1938) n. comb.
D. <u>irregularis</u> Moseley, 1881	S. <u>stejnegeri</u> (Fisher, 1938) n. comb.
D. <u>serpens</u> Broch, 1942	S. <u>purpuratus</u> (Naumov, 1960) n. comb.
D. <u>livida</u> Tenison-Woods, 1879	S. <u>boschmai</u> (Eguchi, 1965) n. comb.
D. <u>gracilis</u> Dana, 1848	S. <u>hattorii</u> (Eguchi, 1968) n. comb.
=D. <u>conferta</u> Quelch, 1885	S. <u>californicus</u> (Verrill, 1866) n. comb.
=D. <u>fragilis</u> Quelch, 1885	S. <u>venustus</u> (Verrill, 1870) n. comb.
=D. <u>granulosa</u> Quelch, 1885	+S. <u>milleri</u> Durham, 1942
=D. <u>milesii</u> Quelch, 1885	S. <u>miniatus</u> (Pourtalès, 1868) n. comb.
D. <u>nitida</u> Verrill, 1864	S. <u>norvegicus</u> (Gunnerus, 1768)
=D. <u>alnuttii</u> Wright, 1882	S. <u>rosaceus</u> (Greef, 1886) n. comb.
=D. <u>brasseyae</u> Wright, 1882	S. <u>blatteus</u> (Boschma, 1961) n. comb.
=D. <u>breviserialis</u> Quelch, 1884	+S. <u>compressus</u> (Römer, 1863)
=D. <u>ochracea</u> Quelch, 1884	= <u>Dendracis pygmaea</u> Römer, 1863
D. <u>coccinea</u> Gray, 1860	= <u>Dendracis multipora</u> Römer, 1863
=D. <u>purpurea</u> Schmeltz, 1875 (nom. nud.)	= <u>Dendracis tuberculosa</u> Römer, 1863
= <u>Lithodendrum saccharatum</u> von Martens, 1902	= <u>Cryptaxis allopoides</u> Reuss, 1865
=D. <u>violacea</u> forma <u>cornuta</u> Broch, 1942	S. <u>subviolaceus</u> (Kent, 1871)
+D. spp. Squires, 1962	S. <u>nobilis</u> (Kent, 1871)
D. <u>borealis</u> Fisher, 1938	=S. <u>explanatus</u> (Kent, 1871)
D. b. <u>japonica</u> Broch, 1942	=S. <u>ochraceus</u> (Quelch, 1884)
+D. <u>parairregularis</u> Eguchi, 1968 (nom. nud.)	S. <u>bithalamus</u> Broch, 1936
D. <u>sulcata</u> Pourtalès, 1867	S. <u>eguchii</u> (Boschma, 1966) n. comb. r
D. <u>foliacea</u> Pourtalès, 1868	S. <u>robustus</u> (Cairns, 1983) n. comb. ? r
D. <u>cervina</u> Pourtalès, 1871	
D. <u>barbadensis</u> Pourtalès, 1874	
D. <u>contorta</u> Pourtalès, 1878	
+D. <u>antigua</u> DeFrance, 1826	
D. (<u>Haplomerismos</u>) <u>anceps</u> Cairns, 1978	
Subfamily Stylasterinae Gray, 1847	
<u>Stylaster</u> (Group A)	<u>Stylaster</u> (Group B)
S. <u>stellulatus</u> Steward, 1878	S. <u>bocki</u> Broch, 1936
S. <u>verillii</u> (Dall, 1884)	S. <u>granulosus</u> Milne Edwards & Haime, 1850
=S. <u>moseleyi</u> (Dall, 1884)	S. <u>bellus</u> (Dana, 1848)
?=S. <u>norvegicus pacificus</u> Broch, 1936	S. <u>sanguineus</u> Milne Edwards & Haime, 1850
S. <u>scabiosus</u> Broch, 1935	=S. <u>tenuis</u> Verrill, 1864
=S. s. <u>infundibiliporus</u> (Eguchi,	

Table 1. Continued

<u>=S. elegans</u> Verrill, 1864	<u>S. e. facies irregularis</u>
<u>S. campylecus</u> (Fisher, 1938)	Hickson & England, 1905
<u>S. c. parageus</u> (Fisher, 1938)	<u>S. e. facies minor</u> Hickson &
<u>S. c. tylotus</u> (Fisher, 1938)	England, 1905
<u>S. c. trachystomus</u> (Fisher, 1938)	<u>S. microstriatus</u> Broch, 1936
<u>S. carinatus</u> Broch, 1936	<u>S. cancellatus</u> Fisher, 1938
<u>S. polyorchis</u> (Fisher, 1938) n. comb.	<u>S. elassotomus</u> Fisher, 1938
?= <u>S. abei</u> (Eguchi, 1968) n. comb.	<u>S. alaskanus</u> Fisher, 1938
<u>S. dentatus</u> Broch, 1936 (junior homonym of <u>S. eximius facies dentatus</u> Hickson & England, 1905, if facies raised to species)	+ <u>S. chibaensis</u> Eguchi, 1954
<u>S. profundiporus</u> Broch, 1936	<u>S. duchassaingii</u> Pourtalès, 1867
<u>S. p. crassicaulis</u> Broch, 1936	= <u>S. elegans</u> Duchassaing & Michelotti, 1864
<u>S. pulcher</u> Quelch, 1884	= <u>S. eximius</u> Kent, 1871
<u>S. divergens</u> Marenzeller, 1904	= <u>S. eximius</u> forma <u>atlanticus</u> Broch, 1936
* <u>S. roseus</u> (Pallas, 1776)	<u>S. filigranus</u> Pourtalès, 1871
<u>S. gemmascens</u> (Esper, 1794)	<u>S. punctatus</u> Pourtalès, 1871
+ <u>S. priscus</u> Reuss, 1872	<u>S. echinatus</u> Broch, 1936
<u>S. profundus</u> (Moseley, 1879)	<u>S. antillarum</u> Zibrowius & Cairns, 1982
<u>S. polymorphus</u> Broch, 1936	<u>S. erubescens</u> Pourtalès, 1868
<u>Stylaster</u> (Group C)	+ <u>S. antiquus</u> Sismonda, 1871
+ <u>S. sp.</u> Tornquist, 1905	<u>S. densicaulis</u> Moseley, 1879
<u>S. amphelioides</u> Kent, 1871	<u>Stylaster</u> (Incertae Sedis)
<u>S. crassior</u> Broch, 1936	<u>S. rossoamericanus</u> Brandt, 1872
<u>S. lonchitis</u> Broch, 1947	nom. nud.
<u>S. ramosus</u> Broch, 1936	+ <u>S. nagaoi</u> (Eguchi, 1968) nom. nud.
<u>S. bilobatus</u> Hickson & England, 1905	* <u>Stylantheca porphyra</u> Fisher, 1931
<u>S. b. facies alba</u> Hickson & England, 1905	<u>S. petrograpta</u> (Fisher, 1938) n. comb.
<u>S. multiplex</u> Hickson & England, 1905	<u>S. papillosa</u> (Dall, 1884) n. comb.
<u>S. flabelliformis</u> (Lamarck, 1816)	* <u>Calyptopora reticulata</u> Boschma, 1968
<u>S. gracilis</u> Milne Edwards & Haime, 1850	<u>C. complanata</u> (Portalès, 1867) n. comb.
<u>S. brunneus</u> Boschma, 1970	= <u>Crypthelia virginis</u> Lindström, 1876
<u>S. papuensis</u> Zibrowius, 1981	<u>C. pachypoma</u> (Hickson & England, 1905)
+ <u>S. mooraboolensis</u> (Hall, 1893)	<u>Stenohelia minima</u> (Hickson & England, 1905)
+ <u>S. sp.</u> Wells, 1977	<u>S. tiliata</u> (Hickson & England, 1905)
<u>S. asper</u> Kent, 1871	<u>S. umbonata</u> (Hickson & England, 1905)
<u>S. incompletus</u> (Tenison-Woods, 1883)	<u>S. conferta</u> Boschma, 1968
<u>S. "eximius"</u>	<u>S. echinata</u> Eguchi, 1968
<u>S. e. facies altus</u> Hickson & England, 1905	<u>S. yabei</u> (Eguchi, 1941)
<u>S. e. facies dentatus</u> Hickson & England, 1905	<u>S. y. forma minor</u> (Eguchi, 1941)

Table 1. Continued

<i>S. robusta</i> Boschma, 1964	<i>C. stenopoma</i> Hickson & England, 1905
<i>S. concinna</i> Boschma, 1964	<i>C. japonica</i> (Milne Edwards & Haime, 1849)
<i>S. profunda</i> Moseley, 1879	<i>C. cryptotrema</i> Zibrowius, 1981
= <i>S. challenger</i> Boschma, 1951	+ <i>C. vetusta</i> Wells, 1977
* <i>S. maderensis</i> (Johnson, 1862)	<i>C. trophostega</i> Fisher, 1938
<i>Conopora</i> (Group A)	<i>C. gigantea</i> Fisher, 1938
<i>C. major</i> Hickson & England, 1905	<i>C. peircei</i> Pourtales, 1867
<i>C. verrucosa</i> (Studer, 1878)	<i>C. affinis</i> Moseley, 1879
= <i>C. pauciseptata</i> Broch, 1951	= <i>C. moseleyi</i> Hickson & England, 1905
<i>C. laevis</i> (Studer, 1878)	<i>C. formosa</i> Cairns, 1983
* <i>C. tenuis</i> Moseley, 1879	<i>C. fragilis</i> Cairns, 1983
= <i>C. obliquus</i> (Studer, 1878)	
<i>Conopora</i> (Group B)	* <i>Astya subviridis</i> (Moseley, 1879)
<i>C. dura</i> Hickson & England, 1909	+ <i>A. nielsen</i> Wells, 1977
+? <i>C. arborescens</i> Nielsen, 1919	Incertae Sedis
<i>Cryptothelia clausa</i> Broch, 1947	+* <i>Congregopora nasiformis</i> Nielsen, 1919
* <i>C. pudica</i> Milne Edwards & Haime, 1849	+ <i>"Astya" crassa</i> (Nielsen, 1919)
<i>C. ramosa</i> Hickson & England, 1905	+ <i>"Stenothelia" boschmai</i> Wells, 1977
<i>C. balia</i> Hickson & England, 1905	<i>"Errina" porifera</i> Naumov, 1960
<i>C. platypoma</i> Hickson & England, 1905	(also listed under <i>Errinopora</i>)

a Cambridge Stereoscan 4-10 microscope; stereo pairs were taken with an 8° tilt of the specimen. The magnifications of all SEM photomicrographs, and therefore most measurements of small skeletal structures, have a $\pm 5\%$ margin of error. All figured specimens are deposited at the USNM unless otherwise noted.

Specimens used for histological examination were first decalcified with a commercial bone decalcification solution (Scientific Products, Decal D 1210) diluted 1:4 with ethanol. This required 1–2 days for small pieces. Decalcified tissue was embedded in paraffin, serial-sectioned at 6 μm thickness, and stained with hematoxylin and eosin. Most of the specimens used were originally fixed and preserved in ethanol; however, fixation in formalin gives better results. In addition, the gastro- and dactylozooids were dissected from decalcified tissue of each genus, processed in a critical point drying apparatus (Denton Vacuum, Inc., DCP-1), and photographed by SEM.

Definitions of terms used to describe stylasterines are found in Fisher (1938), Boschma (1956), and Cairns (in press); however, it is necessary to introduce and resurrect several terms here. The coenosteal texture of most stylasterines is either a *reticulate* maze or a series of straight, parallel, longitudinal bands (*linear*) of calcium carbonate. These bands, termed *coenosteal strips*, are usually between 50–100 μm wide and bordered by thin (5–10 μm) discontinuous grooves or *slits* along and through which coenosteal canals pass. The strips are often sparsely covered by low, rounded, or irregularly shaped granules 7–10 μm in diameter. Some genera are characterized by having linear strips which are not granular but bear rows of imbricated scales, called *platelets*. These two coenosteal textures, referred to as *reticulate-granular* (e.g., pl. 11, fig. B) and *linear-imbricate* (e.g., pl. 14, figs. C–D; pl. 21, figs. D, F, G), respectively, are the most common among the Stylasterina and are, in general, consistent at the generic level. The other two combinations, *reticulate-imbricate* (e.g., pl. 7, figs. B–C) and *linear-granular*, do occur, but are very rare.

Dactylopores often occur as apically perforate mounds or slit spines. If the slit (groove) is on the proximal side of the spine it is termed *adcauline*; if on the distal side of the spine, *abcauline*. Sometimes slit dactylospore spines are *clustered* in groups of 2–5, often resulting in a disordered orientation of the slits. When a spine is enlarged and bears several slits, it is termed *composite*.

The dimensions of a gastrostyle are indicated by a height to width ratio (*H:W*), the width measured at the widest level, exclusive of spines. An *H:W* of 2–4 is considered medium height; less than 2,

squat; over 4, elongate. Gastrostyles are always ornamented with spines, which are tall and *simple*, or *fused* (three or more together, usually aligned on the crest of a ridge). In some species there is a ring of tiny, blunt spines projecting from the wall of the gastropore tube at the level of the gastrostyle tip (e.g., pl. 20, fig. C). This ring, called the *cheval-de-frise* by Fisher (1938) is herein renamed the *ring palisade*. It constricts the gastropore tube into a lower *gastrostyle chamber* and an upper funnel-shaped part leading to the branch surface. In some genera lacking gastrostyles (i.e., *Conopora*, *Astya*, *Crypthelia*), the ring palisade, or its analog, forms a solid ring constricting the gastropore tube into a small flat *lower chamber*, which contains the bulk of the gastrozooid, and a larger, spacious *upper chamber*, into which the dactylozooids enter.

Some genera have fixed *lids* which overhang their cyclosystems; one genus, *Adelopora*, has hinged *opercula*, one concealing each gastropore. Ampullae are usually present as *superficial* hemispheres; less commonly they are completely submerged in the coenosteum (*internal*). Gonophores release their sexual products via *efferent ducts* which are usually seen as small irregular pores on or near the ampulla or, in the case of some female ampullae, as a truncated lateral tube issuing from the side of the ampulla. Dactylozooids are attached to the coenosteal canal network either basally (*simple* dactylozooids) or by a broad "adhesive" base, called *adnate* dactylozooids. In the latter case, a short, free tentacle originates from about the midpoint of the attached base. *Nematopores* are small, shallow pores in the coenosteum which house the *nematophores*, dense concentrations of long, slender nematocysts oriented perpendicular to the branch surface. Nematopores are most common around cyclosystems, especially on pseudosepta and lids, if present.

Species synonymies include only pertinent references, i.e., distributional records or comments of systematic or biologic importance. Exhaustive, but uncritical, synonymies are given by Boschma (1957).

Order STYLASTERINA Family STYLASTERIDAE Gray, 1847 Subfamily Errininae Hickson, 1912

Diagnosis.—Gastro- and dactylopores not arranged in distinct cyclosystems, usually scattered irregularly over coenosteum. If dactylopores are organized into short lines or irregular circles around gastropores (i.e., pseudocyclosystems), the space between the two types of pores is wide and usually additional, randomly placed dactylopores are present.

Lepidopora Pourtalès, 1871

Errina: Pourtalès, 1867: 117 (part).

Pliobothrus: Pourtalès, 1868: 141 (part).

Lepidopora Pourtalès, 1871: 40.—Cairns, in press.

Errina (*Inferiolabiata*): Boschma, 1956: F102 (part).

Errina (*Lepidopora*): Boschma, 1963a: 336.

Diagnosis.—Colonies usually uniplanar but sometimes bushy; branches not coalescent, with pointed, blunt, or clavate branch tips. Coenosteal texture quite variable, including: ornamented by tufts of calcium carbonate along longitudinal ridges; reticulate with tall, slender spines; reticulate with irregular granules; reticulate with rounded granules; linear with granules; and linear-imbricate. Gastro- and dactylopores usually randomly arranged over coenosteum, but sometimes gastropores aligned on anterior branch face and dactylopores aligned on lateral branch edges. Both gastro- and dactylopore tubes long, forming a cluster along each branch axis. Gastropore tube may or may not have a ring palisade. Gastropores sometimes have a lower lip. Gastrostyles cylindrical, without ridges; usually long and slender, with tall, simple spines; H:W usually over 4 and up to 20. Dactylopores usually elevated on small mounds which are apically perforate; pores sometimes linked by ridges; no dactylostyles. Ampullae superficial, large, and hemispherical, sometimes with an efferent tube leading from side. Soft parts unknown.

Discussion.—*Lepidopora* is an extremely variable genus, varying in characters such as: coordination of gastro- and dactylopores, gastrostyle shape, dactylopore shape, colony and branch shape, and especially coenosteal texture. These characters, ordinarily conservative at the generic level, are variable in *Lepidopora*, which leads to the conclusion that it is either an artificially composed, polyphyletic group or perhaps the primitive ancestral stock.

Lepidopora is distinguished from all other genera by its apically perforate dactylopore mounds, nonridged, slender gastrostyles, and large superficial ampullae. No one character distinguishes *Lepidopora* (three other genera have apically perforate dactylopore mounds, three have nonridged styles, and many have superficial ampullae), but these characters taken together are found in all eight species of the genus, and this combination of characters is significantly different from that of any other genus. Boschma (1964a: 61) indicated that *Lepidopora* and *Sporadopora* were very similar, differentiated primarily by the relative height of their dactylopores. They are similar, but, on closer examination, many differences can be found, e.g., the coenosteal texture of *Sporadopora* is different, its gastrostyles are ridged and bear fused spines, it has tabulae, and it has internal ampullae.

Lepidopora, therefore, is considered to be a distinct genus, but an extremely variable one, which, in its range of variation, has characters similar to many other genera in the Errininae, Adeloporinae, and Stylasterinae, especially with regard to coenosteal texture. Because many of its characters are morphologically simple and because it is so variable in otherwise conservative generic characters, it is considered to resemble the primitive genus from which the other stylasterines may have evolved. A discussion of primitive and derived characters and the phylogenetic position of *Lepidopora* will be made in the second paper of this series.

Occurrence.—?Paleocene: Denmark; Recent: North Atlantic, Scotia Ridge, off South Africa, South Pacific, off Antarctica. 84–1,874 m.

Type Species.—*Errina glabra* Pourtalès, 1867, by subsequent designation (Boschma, 1963a: 336).

Lepidopora glabra (Portalès, 1867)

Figure 1A–I

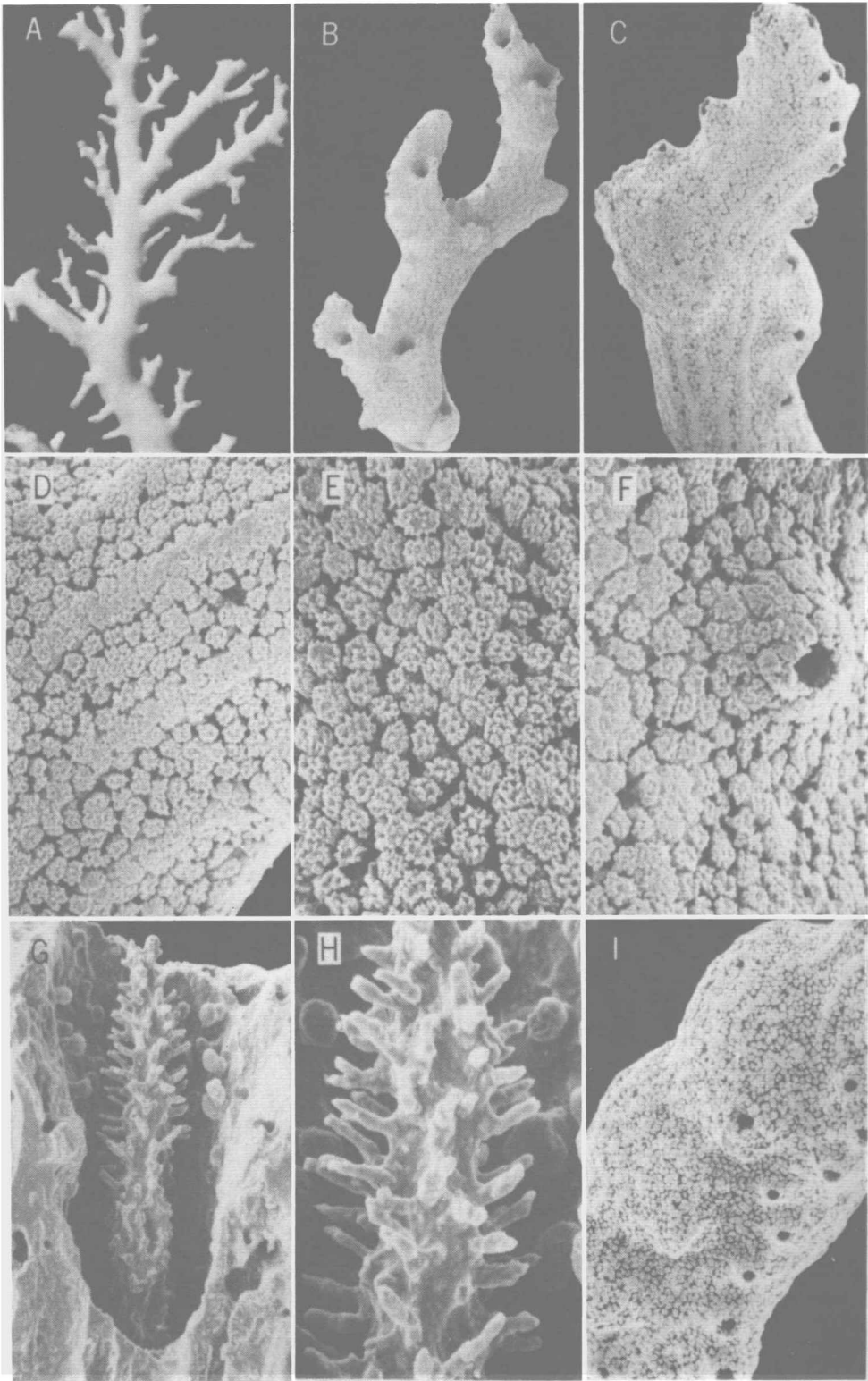
Errina glabra Portalès, 1867: 117.—Boschma, 1957: 54.

Lepidopora glabra: Portalès, 1871: 40, pl. 7, figs. 8–9; 1878: 211.

Errina (Inferiolabiata) glabra: Boschma, 1965: F102, fig. 84, 1a.

Errina (Lepidopora) glabra: Boschma, 1963a: 336, 338; 1963b: 395; 1964a: 60; 1968b: 205.

Diagnosis.—Colonies up to 5.5 cm tall; distal branches slender, pointed, and compressed, about 0.5 mm in diameter; basal branches up to 7 mm in diameter, elliptical in cross section. Coenosteum composed of closely adjacent, irregularly shaped, crystalline (nongranular) tufts of calcium carbonate, each measuring between 21–25 μ m in diameter. Adjacent tufts fuse into slightly elevated longitudinal ridges, which run the length of the branches. Fused ridges about 44 μ m wide and separated by about 0.12 mm of individualized tufts. Gastropores, about 0.2 mm in diameter, occur only on the anterior side of the colony, always bordered by a broad, triangular, abcauline lip. Gastrostyles long and cylindrical (illustrated style 0.42 mm tall, H:W = 9.1), bearing sparse cylindrical spines measuring up to 30 μ m long and 6.5 μ m in diameter. The gastropore tube bears a diffuse ring palisade, the spines measuring up to 30 μ m tall and 25 μ m in diameter. Dactylopores occur



in rows on the lateral branch edges, their centers about 0.2 mm apart. Dactylopore mounds about 110 μm wide, 60–80 μm tall, perforated apically by a pore 30–38 μm in diameter. Ampullae 0.82–0.90 mm in diameter, some with efferent tubules of 0.15 mm diameter.

Discussion.—*Lepidopora*, usually considered a subgenus of *Errina*, was elevated to generic rank by Cairns (in press). The eight species attributed to this genus are listed in Table 1. Representatives of all of these species have been examined by the author.

In his last revision of the subgenus *Lepidopora*, Boschma (1968b) listed four more species than are included in Table 1; however, closer examination has revealed that *E. ramosa* Hickson and England, 1905, and *E. horrida* Hickson and England, 1905, have abcauline slit dactylopore spines and thus belong to *Inferiolabiata*. The description of *L. porifera* (Naumov, 1960) also indicates a placement in *Inferiolabiata* or *Errinopora*. *L. cochleata* (Pourtalès, 1867) has adcauline slit dactylopore spines and is therefore placed in *Errina* s.s.

The type-specimens of *L. carinata* (Pourtalès, 1867) are among the very few Pourtalès coral types that cannot be located at the MCZ. Pourtalès' original and subsequent descriptions (1871) clearly pertain to a species of *Lepidopora*; however, the specimens he identified as *E. carinata* in 1878 belong to *Inferiolabiata*. In view of this confusion, a neotype is designated for *L. carinata* which corresponds very closely to the description of Pourtalès (1871) and was collected near the type-locality: Albatross 2319–2350, 23°10'–11°N, 82°17'–20°W, 60–420 m, USNM 15991 (Fig. 4H–I).

Three species described by Nielsen (1919) from the Paleocene of Denmark (*Sporadopora faxensis*, *Pliobothrus laevis*, and *P. dispersgens*) are not confidently identifiable to genus and may all be referable to *Lepidopora*.

New Records.—ALBATROSS-2152, off Havana, 708 m, USNM 7167; ALBATROSS-2153, 23°10'19"N, 82°23'54"W, 518 m, USNM 15986; ALBATROSS-2161, 23°10'36"N, 82°20'28"W, 267 m, USNM 15987; ALBATROSS-2167, 23°10'40"N, 82°20'30"W, 368 m, USNM 15996; ALBATROSS-2332, 23°10'38"N, 82°20'06"W, 285 m, USNM 16035; ALBATROSS-2333, 23°10'36"N, 82°19'12"W, 309 m, USNM 60511; ALBATROSS-2336, 23°10'48"N, 82°18'52"W, 287 m, USNM 15988; EASTWARD-26537, 27°14.2'N, 79°15.5'W, 520 m, USNM 60353; EASTWARD-26538, 27°12.6'N, 79°13.7'W, 420 m, USNM 60354; EASTWARD-26549, 27°17.5'N, 79°12.5'W, 370 m, USNM 60355.

Distribution.—From the Blake Plateau off Georgia through the Straits of Florida off Havana. 183–1,097 m.

Types.—The syntypes of *L. glabra* are deposited at the MCZ. The largest and best-preserved colony bears the number 3926; five other branches or fragments are present, one of which is numbered 5530. Types examined by the author.

Sporadopora Moseley, 1879

Polypora Moseley, 1876b: 94.

Sporadopora Moseley, 1879a: 429 (nom. nov.); 1881: 93–94.—Broch, 1942: 27–28.—Boschma, 1956: F104.

Figure 1. *Lepidopora glabra* (A, syntype from off Havana, 494 m, MCZ 3926; B–D, F, Eastward-26538: 27°12.6'N, 79°13.7'W, 420 m, 29 Mar. 1975; E, G–I, Albatross-2152: 4 km off Havana, 708 m, 30 Apr. 1884): A, part of syntype colony, $\times 1.5$; B–C, branches showing arrangement of gastro- and dactylopores, $\times 13$, $\times 40$, respectively; D–E, coenosteal texture, $\times 135$, $\times 200$, respectively; F, dactylopore, $\times 185$; G–H, gastrostyle and ring palisade, $\times 135$, $\times 330$, respectively; I, ampullae with efferent tubules, $\times 43$.

Diagnosis.—Colonies uniplanar with occasional anastomosis of branches; branches stout, bluntly tipped, and round in cross section; branch axils U-shaped. Coenosteum irregularly porous to reticulate; if reticulate, coenosteal strips short, discontinuous, and not granular. Gastro- and dactylopores scattered randomly over coenosteum, both usually flush with the surface. Both gastro- and dactylopore tubes long, forming clusters along the branch axis. Long gastropore tubes have multiple, thin, complete tabulae or very fine bridges, which support the gastrostyle. Gastrostyles very long and slender (H:W up to 21) and prominently ridged; dactylostyles absent. Ampullae internal, opening to branch surface by small efferent ducts.

Discussion.—The resemblance of *Sporadopora* and *Lepidopora* noted by Boschma (1964a: 61) has previously been discussed; however, *Sporadopora* is probably most similar to *Distichopora*, particularly the aberrant species *D. providentiae* (Hickson and England, 1909). Originally described as a *Sporadopora*, *D. providentiae* was transferred to *Distichopora* by Broch (1942: 27), this transfer being confirmed by Boschma (1959: 163), the latter author indicating that it was intermediate between the two genera. *D. providentiae* resembles *Sporadopora* by its flabellate corallum and blunt-tipped branches; long, slender (H:W > 10) ridged gastrostyle (a character found only in these two genera); and its low to flush gastro- and dactylopores. Differences include coenosteal texture, shape of dactylopores, and a tendency for the gastropores of *D. providentiae* to be concentrated on the branch edges, flanked by irregular rows of elongate dactylopores. It is the latter character that allies it most closely to *Distichopora*. *D. providentiae* will be discussed again under *Distichopora*.

Occurrence.—?Paleocene: Denmark; ?Miocene: Chatham Island and Victoria, Australia; Recent: Subantarctic South America, New Zealand. 122–1,498 m.

Type Species.—*Polypora dichotoma* Moseley, 1876, by monotypy.

Sporadopora dichotoma (Moseley, 1876)
Figures 2A–H, 24F, 25H, 27A, 28C

Polypora dichotoma Moseley, 1876b: 94–95.

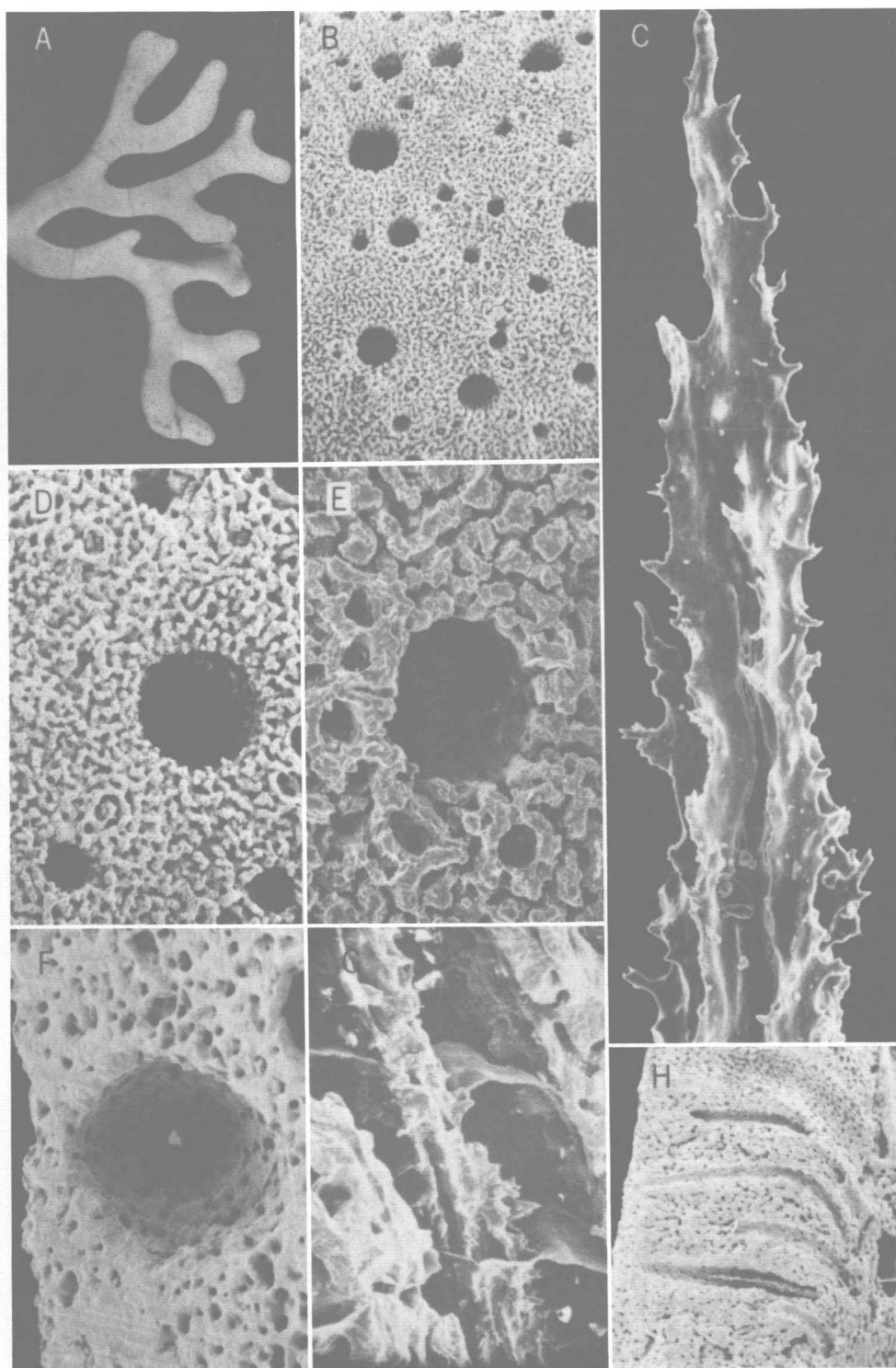
Sporadopora dichotoma: Moseley, 1879: 429–440, pl. 34, figs. 1–2, pl. 35, figs. 1–2, 9, pl. 36, pl. 43, figs. 1–9, 12, pl. 44, figs. 13–14; 1881: 36–47, 83, pl. 1, figs. 1–2, pl. 2, figs. 1–2, 9, pl. 3, pl. 10, figs. 1–9, 12, pl. 11, figs. 13–14.—Weill, 1934: 484, fig. 315a–b.—Boschma, 1956: F104, figs. 85, 3a–b; 1957: 60–61.—Boschma and Lowe, 1969: 15, pl. 5, map 5.—Cairns, in press: figs. 1A–B, 2A–I, 3A–B.

?*Sporadopora dichotoma* Hall, 1898: 177–178.

Diagnosis.—Colonies up to 14 cm tall; distal branches 4–20 mm in diameter, basal branches up to 4.45 cm in diameter. Coenosteum of distal branches homogeneously porous; that of older basal branches composed of short, discontinuous strips in a reticulate pattern. Coenosteum not granulated. Gastropores 0.20–

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Figure 2. *Sporadopora dichotoma* (A, Vema 17–65: 50°18'S, 54°11'W, 1,498–1,501 m, 14 May 1961; B, D, Eltanin-970: 54°59'S, 64°53'W, 586–641 m, 11 Feb. 1964; C, Eltanin-1593: 54°43'S, 56°37'W, 339–357 m, 14 Mar. 1966; E–F, Islas Orcadas 575–34: 54°42'S, 34°51'W, 563–598 m, 19 May 1975; G–H, Hero 715–895: 55°00'S, 64°50'W, 438–548 m, 3 Nov. 1971): A, colony, ×0.56; B, D, arrangement of gastro- and dactylopores, ×15, ×33, respectively; C, tip of gastrostyle, ×167; E, gastropore encircled by ring of shallow pits, ×83; F, cross section of internal ampulla, efferent duct visible in center, ×40; G, gastrostyle supported by tabulae, ×67; H, longitudinal section of branch showing gastrostyle in place, ×12.



0.62 mm in diameter, sometimes surrounded by a ring of 10–15 shallow pits, each about 40–70 μm in diameter. Gastrostyles up to 3.9 mm long, but rarely over 0.20 mm in diameter (H:W to 21); style held in place by thin, complete tabulae. Dactylopores about 0.12 mm in diameter.

Contracted gastrozoid about 0.4 mm in diameter and 1.1 mm long, enveloped by a thin bottle-shaped sheath or sac, which opens to the branch surface. Radiating coenosteal canals extend from the gastrozoid sac for about 1 mm (Fig. 24F). Gastrozooids have 4–7 short tentacles. Dactylozooids dimorphic: larger ones adnate, smaller ones simple. Nematocysts of three sizes: (1) $29.6\text{--}32.7 \times 6.2\text{--}8.6 \mu\text{m}$, and (2) $20\text{--}23 \times 4.7\text{--}6.2 \mu\text{m}$, both types common in gastrovascular cavity of gastrozooids, coenosteal canals, and surface nematophores, and (3) $7.8\text{--}9.0 \times 3.5\text{--}4.0 \mu\text{m}$, common in dactylozooids and coenosteal canals.

Discussion.—The skeleton of *S. dichotoma* has been described and illustrated in greater detail by Cairns (in press), and Moseley (1879, 1881) has beautifully illustrated and described the soft parts. I can only add that Moseley reported two size classes of nematocysts ($40\text{--}42 \times 6.6\text{--}7.7 \mu\text{m}$ and $15.7\text{--}16.2 \times 6.6 \mu\text{m}$), both of which are larger than the nematocysts reported here. Also, the number of gastrozoid tentacles, reported as four by Moseley, ranges to seven per gastrozoid.

Three other species are assigned to *Sporadopora*, only one of them being Recent, *S. mortenseni* Broch, 1942. Known only from the New Zealand region at 122–282 m, it is distinguished from *S. dichotoma* by its more delicate colony form, more solid coenosteum, incomplete tabulae, and smaller gastropores (Cairns, in press). The two fossil species are *S. marginata* Tenison-Woods, 1880, known only from the Miocene of Chatham Island, and *S. faxensis* Nielsen, 1919, known only from the Danian of Fakse, Denmark (Lower Paleocene). A figured syntype of *S. faxensis* was examined (deposited at the Copenhagen Geologisk Museum, MMH 1750). It differed from Recent *Sporadopora* by having superficial ampullae and a smooth coenosteal texture. The preservation was not adequate to determine the presence or absence of gastrostyles, and dactylopores were not noted. In view of its differences from Recent *Sporadopora* and its poor preservation, it is possible that this species could belong to *Sporadopora*, *Lepidopora*, or *Pliobothrus*.

According to Boschma (1957), the types of *S. marginata* are no longer in existence; from the original description, Boschma (1964a) doubted its placement in *Sporadopora* but was unable to place it in any genus with certainty.

Two other species have been incorrectly assigned to *Sporadopora*. *S. providentiae* Hickson and England, 1909 was transferred to *Distichopora* by Broch (1942) (also see Boschma, 1959), and *S. cleithridium* Squires, 1958 was transferred by Squires (1962) to the milleporine genus *Axoporella*. *Axoporella* has subsequently been synonymized with *Axopora* and placed in a separate order, the Axoporina (Boschma, 1963c).

Distribution.—Off Uruguay; Falkland Rise; Scotia Ridge from Tierra del Fuego to South Georgia; South Shetland Islands. 250–1,498 m.

Types.—Syntypes of *S. dichotoma* are deposited at the BM (1880.11.25.166–168, 1957.2.28.42). Specimens examined by the author.

Pliobothrus Pourtalès, 1868

Pliobothrus Pourtalès, 1868: 141.—Moseley, 1881: 94.—Broch, 1942: 32–33 (part).—Boschma, 1956: F104.

Steganopora Hickson and England, 1905: 26.

Diagnosis.—Branching uniplanar and nonanastomosing; branches round in cross section or flattened in flabellar plane. Coenosteum composed of longitudinal strips

covered by imbricated platelets of variable width. Strips bordered by large, elongate coenosteal pores. Dactylopore coenosteum may be coarsely granulate. Gastro- and dactylopores irregularly scattered; however, usually slightly more abundant on anterior side. Gastropores round to slightly elliptical, flush with surface, opening in to a larger, roughly hemispherical chamber below (Fig. 3I). Rudimentary, perforate tabulae sometimes occur in the gastropore tube. Dactylopores apically located on tall tubes or low mounds; dactylopore tubes extend along center of branch axis for a considerable distance. No gastro- or dactylostyles. Ampullae usually internal and hemispherical, opening to surface by a small efferent pore. No sexual dimorphism in size was noted.

Discussion.—*Pliobothrus* and *Phalangopora* are the only two genera in the Errinae that lack gastrostyles. They also have linear-imbricate coenosteal texture, but otherwise differ in many characters: i.e., *Pliobothrus* has large coenosteal pores, rudimentary gastropore tabulae, apically perforate dactylopores, randomly placed gastro- and dactylopores, internal ampullae, clustered axial dactylopore tubes, and a less uniform imbrication of coenosteal platelets. Most of these character states are considered as more simple than those of *Phalangopora* and therefore *Pliobothrus* is provisionally grouped with *Sporadopora* and *Lepidopora* as among the most primitive of the stylasterine genera.

Occurrence.—?Paleocene: Denmark; Recent: North Atlantic, Indonesia. 80–1,097 m.

Type Species.—*Pliobothrus symmetricus* Pourtalès, 1868, by subsequent designation (Kühn, 1928).

Pliobothrus symmetricus Pourtalès, 1868
Figures 3A–H, 24G, 25G, 27B

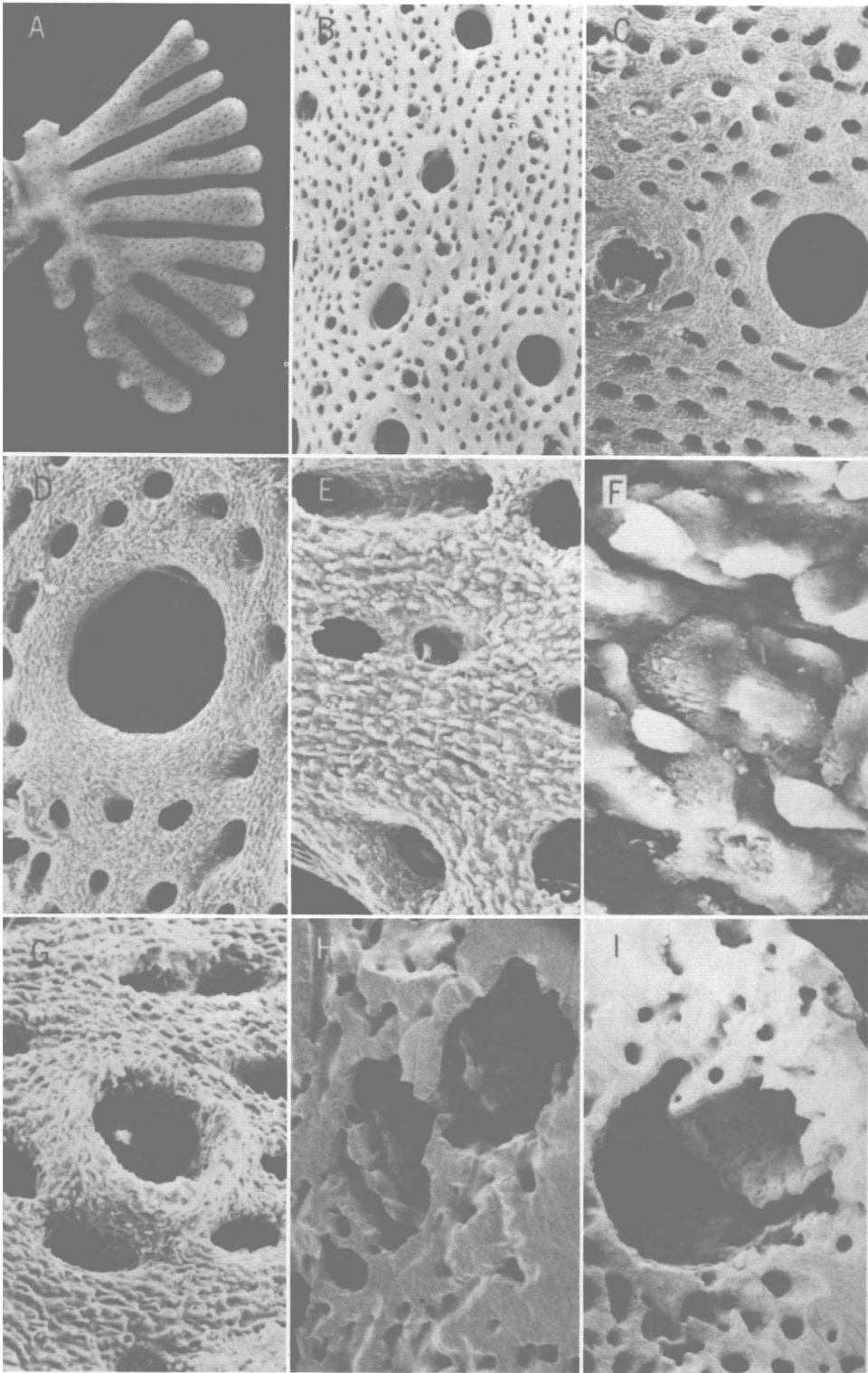
Pliobothrus symmetricus Pourtalès, 1868: 141.—Duncan 1870: 297.—Portalès, 1871: 57, pl. 4, figs. 7–8.—Duncan, 1873: 336, pl. 49, fig. 7.—Portalès, 1878: 211.—Moseley, 1881: 47–50, 84, pl. 8, figs. 2–3.—Agassiz, 1888: 138–139, fig. 444.—Nutting, 1895: 177.—Hickson, 1912b: 465–466.—Broch, 1914: 3–7, pl. 1, figs. 1–3, pl. 3, figs. 19–20, 28–29, pl. 4, figs. 34, 40–42.—Dons, 1939: 196–197, figs. 1–2.—Boschma, 1956: F104, figs. 85, 1a–b; 1957: 59–60.—Squires, 1965: 24, pl. 2, figs. 7–8.—Boschma, 1967: 333–335, pl. 1, figs. 5–6.

Pliobothrus n. sp. Moseley, 1876a: 548.

Diagnosis.—Colonies up to 5 cm tall and 8 cm broad; branch tips blunt, sometimes clavate, up to 6 mm in greater diameter. Coenosteal strips 80–90 μ m wide, platelets 4–11 μ m wide. Coenosteal pores about 45 μ m wide and up to 170 μ m long. Gastropores 0.35–0.41 mm in diameter. Dactylopores 90–110 μ m in diameter, raised on mounds up to 0.1 mm tall. Ampullae 0.80–0.90 mm in diameter.

Gastrozooids with at least five small tentacles; mouth cruciform. Dactylozooids simple, with central lumen. Nematocysts of two kinds: larger nematocysts (39.3–43.8 \times 7.8–12.5 μ m) are common in coenosteal canals and epithelium; smaller (8.0–9.5 \times 3.0–3.2 μ m) are very rare in ectoderm of gastrozooid. Each male ampulla contains one compound gonophore, i.e., a compartmentalized mass containing “pseudofollicles” (Broch, 1914), each of which contains sperm of varying degrees of development. Male spadix bifurcate.

Discussion.—Because of the detailed studies of Moseley (1881) and Broch (1914), *P. symmetricus* is one of the morphologically best known stylasterine corals. However, both authors failed to detect the tiny gastrozooid tentacles, at least five of which occur on each polyp, as Moseley (1881: 48) indicated for the closely related *P. tubulatus*. Otherwise, little can be added to the histological analyses of these two workers.



Four other species are assigned to the genus *Pliobothrus*. *P. tubulatus* (Pourtalès, 1867), known only from the Greater Antilles at 493–704 m, differs from *P. symmetricus* in having much taller, granulated, dactylopore tubes (up to 0.65 mm tall) and more slender, pointed branches. *P. spinosa* (Hickson and England, 1905), known only from the type-locality off Halmahera, Indonesia at 1,089 m, was originally described as the basis of the new genus *Steganopora*. Broch (1914) synonymized it with *Pliobothrus*, but Boschma (1956; 1957) treated it as a monotypic genus. Unfortunately the type, and only known specimen, of *P. spinosa* is lost (personal communication, van Soest, 1981); however, its description is remarkably similar to *P. tubulatus*, differing primarily in its even longer dactylopore tubes and superficial ampullae. Two other species, *P. dispersens* and *P. laevis* are known only from their type-locality of the Danian of Faxe, Denmark (Lower Paleocene). A figured type and a topotypic specimen of *P. laevis* were examined (Copenhagen Geologisk Museum, MMH 1757); both were shown to have large hemispherical ampullae, smooth coenosteum, apically perforate dactylopore mounds, and low, elliptical gastropores. Types of *P. dispersens* (Copenhagen Geologisk Museum, MMH 1756) have reticulate coenosteum, apically perforate dactylopore mounds, low gastropores, and no ampullae. In both cases the preservation was not adequate to distinguish gastrostyles, if present at all, and for this reason both species are not identifiable as to genus and may well belong to *Lepidopora*, instead. Other species referred to *Pliobothrus* included *P. grantmackiei* Squires, 1965, which is herein assigned to the bryozoan genus *Porina* (personal communication, A. Cheetham, 1981), and *P. seriatus* Broch, 1942, a junior synonym of *Phalangopora regularis* Kirkpatrick, 1887.

New Records.—ALBATROSS-2660, 28°40'N, 78°46'W, 921 m, USNM 60361; SILVER BAY-2418, 24°15'N, 81°24'W, 265–293 m, USNM 60359; OREGON-1348, 24°29'N, 81°50'W, 274 m, USNM 60357; GERDA-702, 26°29'N, 78°39'W, 73–220 m, USNM 60358; Johnson-Smithsonian Deep-Sea Expedition-43, 18°02'N, 67°51'W, 439–549 m, USNM 60360, SABP, BLM-3F, 31°46'N, 79°05'W, 540 m, USNM 49141; SABP, BLM-2H, 32°20'N, 78°10'W, 411 m, USNM 49130, 49131; off Sombrero Light, Pourtalès Plateau, 73–210 m, USNM 60356.

Distribution.—North Atlantic: Sombrero, D.W.I.; Mona Island; Straits of Florida; Bahamas; Blake Plateau to South Carolina; Iceland; off Norway; Faeroe Channel; Azores. 80–1,097 m.

Types.—Two syntypes are deposited at the MCZ. The larger colony from Bibb-64 (illustrated by Pourtalès, 1871: pl. 4, fig. 7) is designated lectotype (MCZ 5529), the other specimen as paralectotype (MCZ 5550). Both were examined by the author.

Cheiloporidion Cairns, in press

Cheiloporidion Cairns, in press.

Diagnosis.—Colonies uniplanar with a strong tendency toward branch anastomosis, producing a network of irregularly shaped fenestrae. Branches elliptical to

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Figure 3. *Pliobothrus symmetricus* (A, lectotype from Bibb-64: 24°17'N, 81°43'W, 262 m, 11 May 1868, MCZ 5529; B–G, off Marathon, Florida, USNM 49692; H, Oregon-1348: 24°29'N, 81°50'W, 273 m, 18 July 1955): A, colony, ×0.9; B, arrangement of gastro- and dactylopores, ×19; C, gastropore on right and opening of efferent duct on left, ×43; D, gastropore surrounded by coenosteal pores, ×67; E–F, coenosteal texture, ×167, ×1,530, respectively; G, dactylopore, ×175; H, longitudinal section of a gastropore containing several porous tabulae, ×33. *Pliobothrus tubulatus*: I, Albatross-2152: 4 km off Havana, 708 m, 30 Apr. 1884, longitudinal section of a gastropore tube, ×50.

rectangular in cross section, the greater axis perpendicular to the plane of branching. Branches ridged on both anterior and posterior faces. Coenosteum reticulate, composed of short discontinuous strips, which are smooth (not granulate) and have rounded edges. Dactylopores occur randomly on anterior and lateral branch surfaces; gastropores loosely aligned along lateral edges. Gastro- and dactylopore tubes short, branches compact. Gastropores flush with branch surface; gastrostyles ridged, bearing fused spines. Dactylopores rimmed by two to four vertical platelets, which form a discontinuous collar around the pore; no dactylostyles. Ampullae superficial. Soft parts unknown.

Discussion.—*Cheiloporidion* has several characters not shared with any other genera, i.e., low, rimmed dactylopores composed of platelets; a nongranulate (smooth), reticulate coenosteal texture; and a very short gastrostyle, which is supported by a very broad base. Its resemblance to *Errinopsis* in colonial form is probably convergent. It is placed near the more primitive genera because of its lack of coordination of gastro- and dactylopores and its relatively simple dactylopore structure.

Occurrence.—Recent: Argentina to Tierra del Fuego. 642–1,137 m.

Type Species.—*C. pulvinatum* Cairns, in press, by original designation.

Cheiloporidion pulvinatum Cairns, in press

Figure 4A–G

N. gen., n. sp. Boschma and Lowe, 1969: 15, pl. 5, map 4.

Cheiloporidion pulvinatum Cairns, in press: figs. 11A, 12A–F.

Diagnosis.—Holotypic colony a fragment 5.7 cm broad and 3.5 cm tall. Ratio of length to width of branch cross section up to 2; intermediate-sized branch measures 6.2×3.4 mm in diameter. Posterior sides of distal branches carinate; anterior sides also bear discontinuous and coarser ridges. Coenosteal strips 50–65 μ m wide; coenosteum light pink. Gastropore 0.17–0.40 mm in diameter. Gastropore tube consists of a spherical gastrostyle chamber which leads, via a slight constriction (but no ring palisade), to a funnel-shaped upper tube that opens to the surface. Gastrostyle massive and squat, composed of a wide, cylindrical basal main shaft, which abruptly tapers to a lesser diameter at the constriction, and finally to a point at the branch surface. The illustrated gastrostyle is 0.49 mm tall and 0.35 mm broad, basally (H:W = 1.4). Dactylopores 47–80 μ m in diameter; surrounding collar up to 65 μ m tall. Internal diameter of ampullae 0.42–0.70 mm.

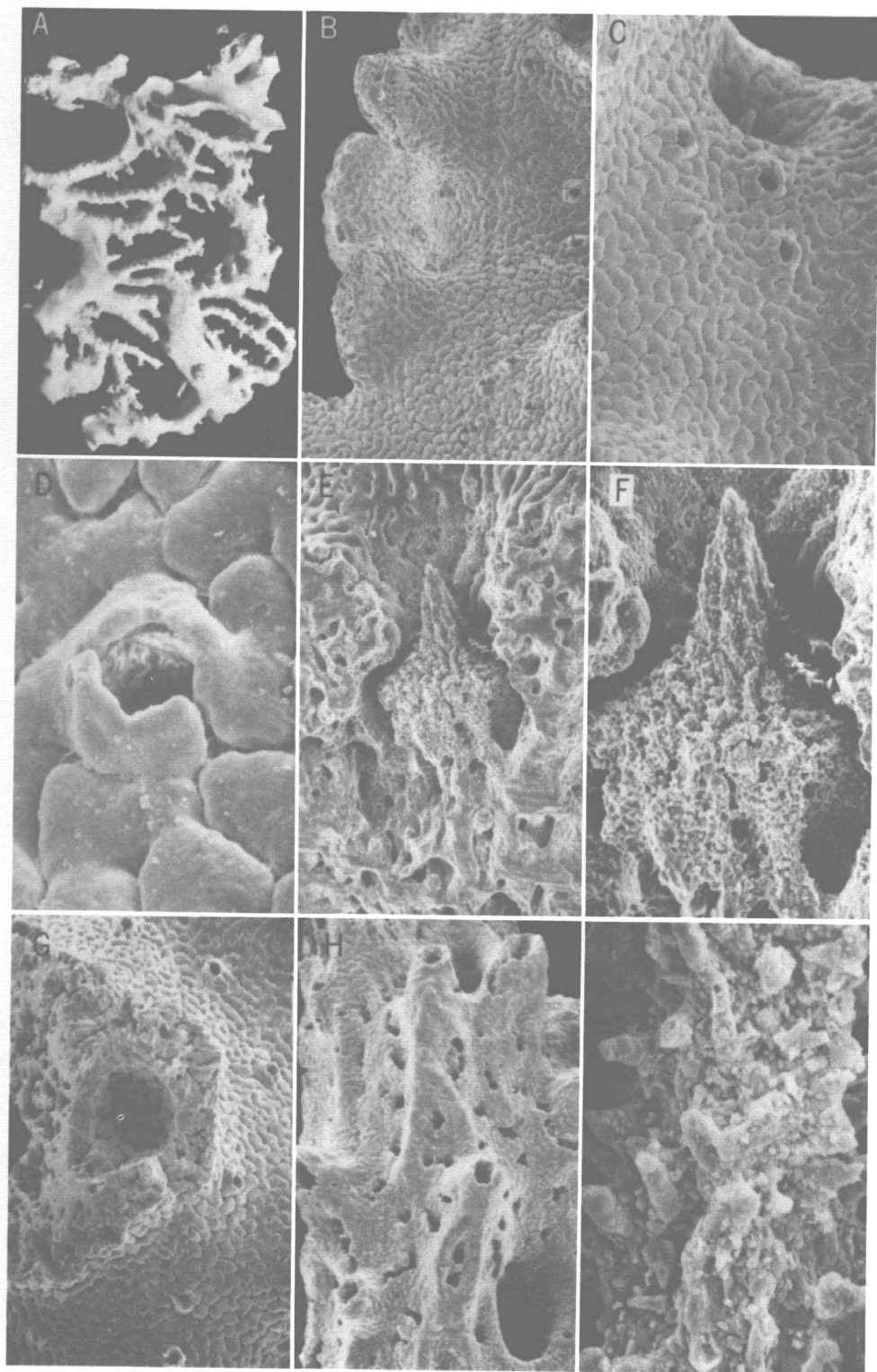
Discussion.—*Cheiloporidion* is a monotypic genus. It is more fully described and illustrated by Cairns (in press).

Distribution.—Off Argentina; off Cape Horn, Tierra del Fuego. 642–1,137 m.

Types.—Holo- and paratypes deposited at the USNM.

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Figure 4. *Cheiloporidion pulvinatum* (A–G, holotype from Vema 17-RD14: 38°58'S, 55°17'W, 595–642 m, 19 June 1961): A, colony, $\times 1$; B, discontinuous branch carina, $\times 29$; C, reticulate coenosteal texture and dactylopores, $\times 50$; D, dactylopore, $\times 230$; E–F, gastropore containing gastrostyle, $\times 60$, $\times 125$, respectively; G, cross section of internal ampulla, $\times 33$. *Lepidopora carinata* (neotype from Albatross 2319–2350: 23°10'31"N, 82°17'45"W, 60–421 m, 17–20 Jan. 1885): H, gastro- and dactylopores, $\times 120$; I, gastrostyle, $\times 500$.



Lepidotheca new genus

Errina: Hickson and England, 1905: 18–19 (part).—Boschma, 1957: 49 (part).—Eguchi, 1968: 47.

Errina (Errina): Hickson, 1912a: 880 (part).

Errina (Labiata): Broch, 1942: 39, 57 (part).

Errina (Inferiolabiata): Boschma, 1956: F102 (part); 1963a: 337–338 (part); 1964e: 294 (part).

Errina (Lepidopora): Boschma, 1963a: 338 (part).

Diagnosis.—Colonies flabellate and usually delicate; branches do not anastomose. Coenosteal texture linear-imbricate. Gastro- and dactylopores randomly distributed, but predominantly on the anterior side, or with gastropores located at or near branching axils. Gastropores round to elliptical, sometimes bordered by an abcauline lip. Gastrostyles long and slender ($H:W = 4-9$) and usually not ridged, resembling those of *Lepidopora*; however, the styles of several species are slightly ridged. Ring palisade usually present. Dactylopore spines low, horseshoe-shaped structures usually strongly inclined toward the distal branch tip. Walls of dactylopore spines thin, the slit usually occupying over half the width of the spine. Slits of spines abcauline, always facing the top of the colony. Spines well separated from one another, never clustered or composite, and never ridged. Dactylostyles usually absent; only *L. tenuistylus* has dactylostyles, similar to those of *Inferiolabiata*. Ampullae large superficial hemispheres.

Discussion.—Most of the seven species referred to *Lepidotheca* were previously assigned to *Errina (Inferiolabiata)*, a catchall genus for all *Errina* with distally directed (abcauline) dactylopore spine slits. As stated in my discussion of *Inferiolabiata*, these seven species constitute a discrete genus having its closest affinities with *Inferiolabiata*. To reiterate, *Lepidotheca* differs from *Inferiolabiata* by its linear-imbricate coenosteal texture (vs. reticulate-imbricate); consistently flabellate colony form (vs. tendency towards bushy); lack of dactylostyles (except for *L. tenuistylus*); and short, nonridged, horseshoe-shaped dactylopore spines, which are always well separated (vs. tall, ridged, spout-like spines, which are often clustered or fused together).

Etymology.—The generic name refers to the scale-like coenosteal texture produced by the imbricate platelets. Gender: feminine.

Occurrence.—Recent: off Mauritius, Indonesia, Japan, New Zealand, Subantarctic, Greater Antilles. 85–2,010 m.

Type Species.—*Errina (I.) fascicularis* Cairns, in press, here designated.

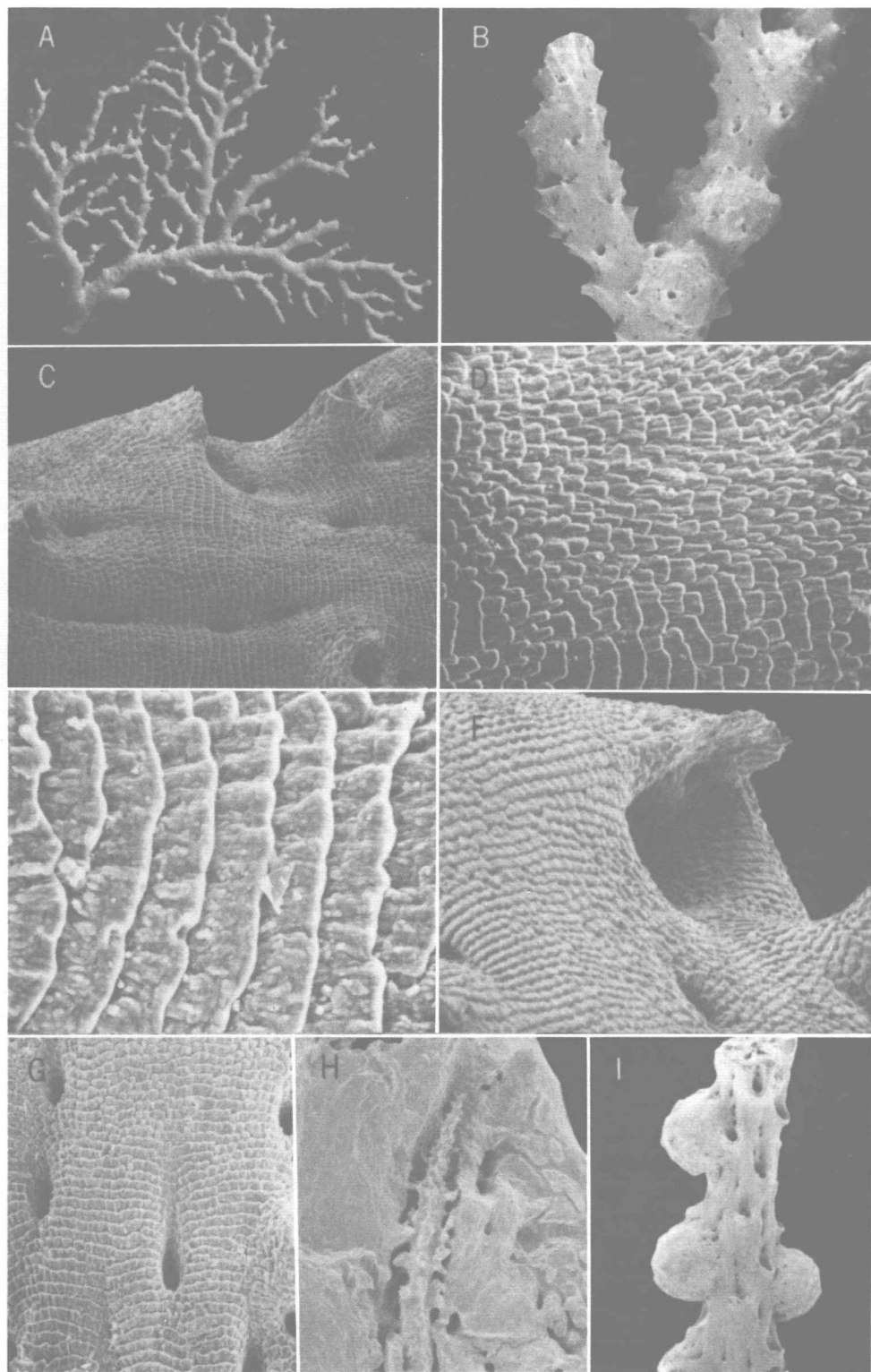
Lepidotheca fascicularis (Cairns, in press)

Figures 5A–I, 24E, 25E

Errina (Inferiolabiata) fascicularis Cairns, in press: figs. 22H, 29A–K, 30A–E.

Diagnosis.—Colonies extremely delicate, up to 6 cm tall with a basal branch diameter of 9.2 mm. Longitudinal coenosteal strips slightly convex and broad

Figure 5. *Lepidotheca fascicularis* (A–C, F, H, Eltanin-1423: 56°21'S, 158°28'E, 1,574–1,693 m, 12 Feb. 1965; D, Gazelle 66/44: 35°21'S, 175°40'E, 1,092 m, 12 Nov. 1875, Museum für Naturkunde, Berlin; E, G, I, Eltanin-684: 54°55'S, 38°05'W, 595–677 m, 25 Aug. 1963): A, holotype colony, $\times 1$; B, branch tip bearing ampullae, $\times 12$; C, gastropore lip and several dactylopores, $\times 51$; D–E, imbricate coenosteal texture, $\times 133$, $\times 333$, respectively; F, gastropore lip, $\times 67$; G, coenosteal texture and coenosteal pores, $\times 67$; H, gastrostyle, $\times 33$; I, branch with ampullae, $\times 12$.



(0.25–0.38 mm wide), becoming less apparent toward branch tips. Width of platelets variable: some very broad, extending from slit to slit across a strip, others quite slender (13 μ m wide); approximately 40–45 leading edges of platelets occur per mm. Gastropores invariably occur at branch axils, and occasionally on lateral branch surfaces. Those occurring at axils are often flanked by two lips; those on the sides are bordered by an abcauline lip. Gastrostyle composed of a slender, spinose, distal section and a much longer and wider, non spinose basal part, which are separated by a tabula. The distal section is 0.25–0.43 mm long and 0.07–0.08 mm in diameter (H:W = 3.3–6.1), sparsely ornamented with blunt, often fused, spines up to 25 μ m tall, which are vertically aligned. The entire style measures up to 1.31 mm long and 0.12 mm in diameter (H:W = 11). No ring palisades. Dactylopore spines 0.15–0.20 mm tall and 0.18–0.25 mm wide, usually located along coenosteal slits or on ampullae. Female ampullae 0.98–1.10 mm in diameter; male, 0.77–0.82 mm in diameter.

Gastrozooids cylindrical with an almost square, concave (when preserved) hypostome, one tentacle corresponding to each corner of the square. Dactylozooids simple. Neamtocysts measuring $6.0\text{--}7.0 \times 2.5\text{--}3.5 \mu\text{m}$ are very common in gastro- and dactylozooids tentacle tips.

Discussion.—The other six species of *Lepidotheca* are briefly diagnosed. *L. cervicornis* (Broch, 1942): branches coarse; gastro- and dactylopores randomly dispersed; however, gastropores always bordered proximally by a dactylopore spine; gastrostyle slightly ridged (H:W about 5); off New Zealand (101 m). *L. tenuistylus* (Broch, 1942): branches delicate; gastro- and dactylopores randomly distributed; no gastropore lips; rudimentary dactylostyles present; gastrostyle not ridged (H:W about 6); Mauritius (238–274 m). *L. ramosa* (Hickson and England, 1905): branches delicate, gastropores below axils on anterior side bordered by a large abcauline lip; Suva Sea, Indonesia (520 m). *L. horrida* (Hickson and England, 1905): very similar to *L. fascicularis* but with smaller, carinate dactylopore spines; Djilolo Passage, Indonesia (1,089 m). *L. japonica* (Eguchi, 1968): branches coarse; gastro- and dactylopores randomly distributed; no gastropore lip; H:W of gastrostyle about 6.9; Sagami Bay, Japan (85 m). *L. hachijoensis* (Eguchi, 1968): branches delicate; gastro- and dactylopores randomly distributed; no gastropore lip; H:W of gastrostyle about 6; dactylopore spines very low (flush on basal branches); Sagami Bay (200 m). The types of all but the last two species have been examined by the author.

Distribution.—Subantarctic. 540–2,010 m.

Types.—Holotype and most paratypes deposited at USNM. One paratype at BM.

Phalangopora Kirkpatrick, 1887

Phalangopora Kirkpatrick, 1887: 212.—Boschma, 1956: F104.

Pliobothrus: Broch, 1942: 33–36.

Diagnosis.—Branching uniplanar and nonanastomosing; branches round in cross section and blunt tipped. Coenosteum composed of longitudinal strips covered by narrow, imbricate platelets of relatively uniform width. Strips delimited by narrow, elongate pores. Gastropores linearly arranged on both flabellar faces, each bordered by a broad abcauline lip. Elongate dactylopores linearly arranged on branch edges, and more highly raised on abcauline side. Branch core dense, permeated by narrow diameter coenosteal canals. Gastropore tubes short; dactylopore tubes long and slender, but do not form clusters of tubes in branch axis; no tabulae

present. No gastro- or dactylostyles. Female ampullae large, superficial. Male colonies unknown.

Discussion.—Broch (1942: 33) indicated that *Phalangopora* was morphologically intermediate between *Pliobothrus* and *Inferiolabiata*; he finally placed the type-species of *Phalangopora* in *Pliobothrus* and *P. seriatus*. I basically agree with Broch's interpretation: *Phalangopora* has characters in common with both *Pliobothrus* and *Inferiolabiata* (my *Lepidotheca*) but is also sufficiently different from both to be treated as a separate genus. I previously compared it to *Pliobothrus* in the discussion of that genus. *Phalangopora* is similar to *Lepidotheca* in coenosteal texture, presence of a lower gastropore lip and superficial ampullae, and shape of dactylopore. It differs primarily in its lack of a gastrostyle and its linear arrangement of gastro- and dactylopores.

Occurrence.—Recent: Mauritius. 238–274 m.

Type Species.—*P. regularis* Kirkpatrick, 1887, by monotypy.

Phalangopora regularis Kirkpatrick, 1887
Figures 6A–H, 25D, J

Phalangopora regularis Kirkpatrick, 1887: 212–214, pl. 8, figs. 1–5. —Broch, 1951b: 126. —Boschma, 1956: F104, figs. 85, 2a–c; 1957: 59.

Pliobothrus seriatus Broch, 1942: 33–36, pl. 3, fig. 10, text-fig. 9.

Diagnosis.—Colonies up to 6 cm tall and 7 cm broad; branches bluntly tipped, about 1 mm in diameter distally, increasing up to 3.5 mm in diameter at the basal attachment. Branch axils often U-shaped; occasionally distal branches strongly recurved. Coenosteal strips 85–120 μm wide; platelets about 12 μm wide, such that 5–10 adjacent platelets comprise the width of a strip at any point. Coenosteal pores elongate, about 16 μm wide. Gastropores, measuring about 0.2 mm across, occur approximately every 1 mm; dactylopores occur about every 0.33 mm. Isolated or short rows of dactylopores sometimes occur on the flabellar faces. Dactylopores are elongate in the direction of the branch, about 0.15 mm long, 0.06 mm wide, and elevated about 0.11 mm at the proximal edge. Female ampullae prominent, up to 1.5 mm in diameter, occurring singly and in clusters. The majority of ampullae (68/81 of the holotype's) occur on the posterior side. A small, round depression, about 0.2 mm in diameter, occurs on some ampullae (? incipient efferent duct).

Gastrozooids with 0–6 tentacles. Dactylozooids dimorphic: isolated individuals, large and simple; those in series, smaller and adnate. Nematocysts of only one size (7.0–8.5 μm \times 4.0–4.5 μm) common in coenosteal canals and dactylozooids.

Discussion.—*Phalangopora* is a monotypic genus. There is no doubt that *Pliobothrus seriatus* Broch, 1942 is a junior synonym.

Distribution.—Known only from three localities off Mauritius, 238–274 m.

Types.—The holotype of *P. regularis* is deposited at the BM (1891.12.12.1). The types of *P. seriatus* are deposited at the Zoologisk Museum, Copenhagen. Both types examined by the author.

Inferiolabiata Broch, 1951

Errina: Moseley, 1879: 443–447 (part).

Errina (*Errina*): Hickson, 1912a: 880 (part).

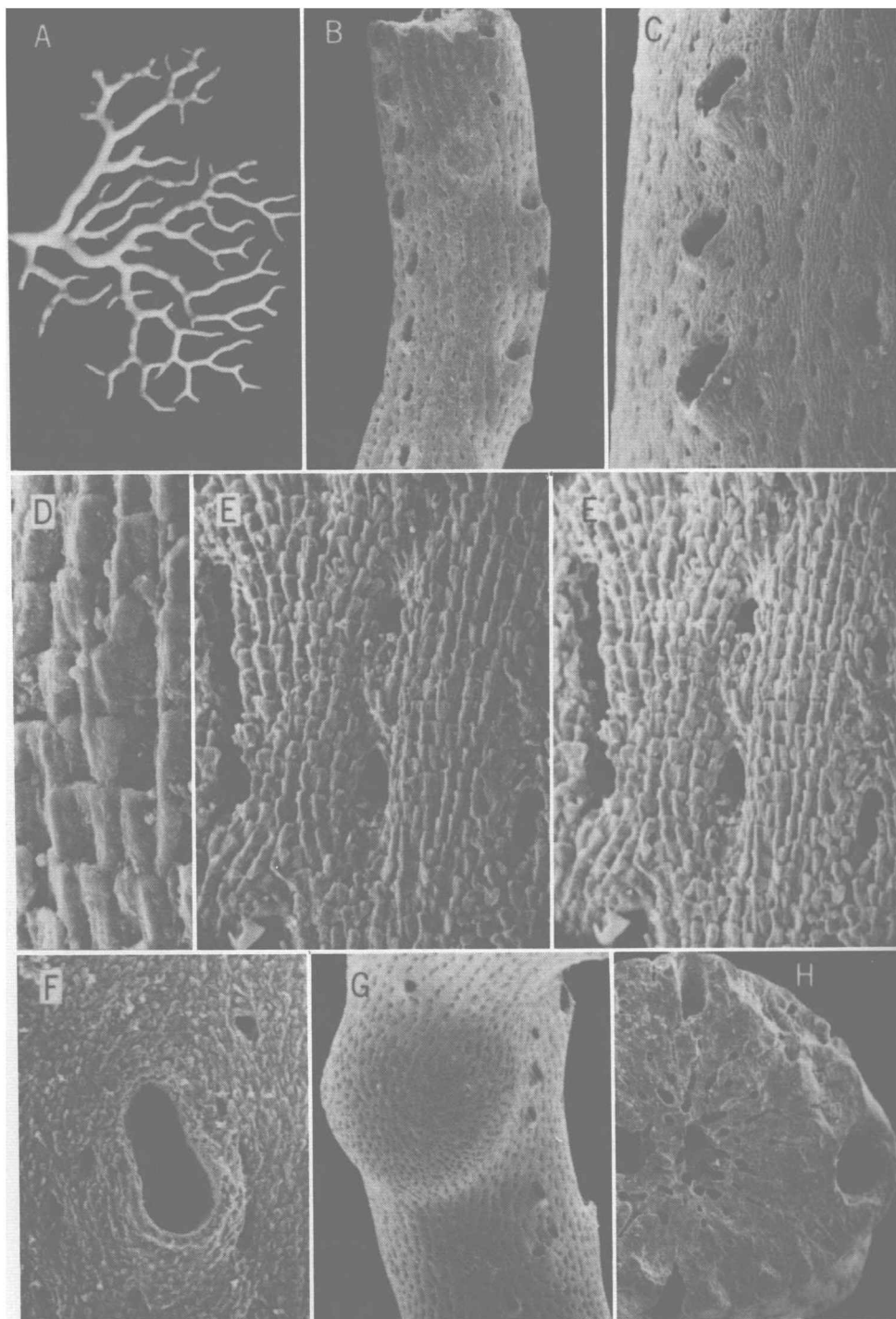


Figure 6. *Phalangopora regularis* (A-H, holotype from off Mauritius, BM 1891.12.12.1): A, holotype colony, $\times 0.75$; B, branch showing arrangement of gastro- and dactylopores, $\times 20$; C, row of dactylopores, $\times 50$; D-E, coenosteal texture, $\times 670$, $\times 200$, respectively, E is a stereo pair; F, dactylopore, $\times 133$; G, branch with ampullae, $\times 19$; H, cross section of branch, $\times 47$.

Errina (*Labiata*) Broch, 1942: 39 (part).

Errina (*Inferiolabiata*) Broch, 1951b: 125 (pro *Labiata*).—Boschma, 1956: F102 (part); 1963a: 337 (part); 1965b: 21 (part).

Diagnosis.—Colonies flabellate to bushy; branches round in cross section and blunt tipped, sometimes anastomosing in response to a polychaete worm symbiosis. Coenosteal texture reticulate-imbricate, the reticulation sometimes obscure away from base; no granules. Gastro- and dactylopores randomly distributed; gastropores round and not lipped. Gastrostyles cylindrical, gradually attenuate, and not ridged ($H:W = 3-10$). Styles bear large individual spines and may be held in place by tabulae. Dactylopore spines tall (up to 0.7 mm) and spout-like, with an abruptly truncated tip. Dactylopore spines grooved along the side facing top of colony (abcauline); lower side of spine longitudinally ridged. Adjacent spines often joined at their edges, forming a tier of 2–5 fused spines encircling part of the branch. Dactylopores bear 1–4 rudimentary dactylostyles. Ampullae large superficial hemispheres.

Discussion.—*Inferiolabiata* has, in the past, been treated as a subgenus including those 12 species of *Errina* s.l. which have abcauline slit dactylopore spines. However, when examined more closely, this artificial assemblage of species can be divided into three groups, each of which is considered a distinct genus. The type-species, *I. labiata*, limits the genus to only two species, it and *I. lowei* Cairns, in press. *I. echinata* (Moseley, 1879) defines a second, monotypic genus, *Stellapora*, and seven species are placed in the new genus, *Lepidotheca*. The remaining two species, *Spinipora irregularis* and *Labiopora lobata*, both described by Nielsen (1919) and placed in *Inferiolabiata* by Boschma (1964e), are reattributed to *Errina* s.s. and *Errinopora*, respectively. The only characters that all three genera have in common are the presence of abcauline grooved dactylopore spines and large superficial ampullae. *Inferiolabiata* differs from *Lepidotheca* by its reticulate-imbricate coenosteum (vs. linear-imbricate), 1–4 dactylostyles per dactylopore (vs. none), and very tall, ridged, spout-like dactylopore spines which are often fused together (vs. short, smooth, horseshoe-shaped dactylopore spines which are always separate). It differs from *Stellapora* in coenosteal texture and in the shapes of its gastropore, gastrostyle, and dactylopore spines. The only other genus in the Errinae to have both gastro- and dactylostyles is *Errinopora*; however, the resemblance appears to be superficial as the two genera differ in many other characters.

Occurrence.—Recent: Antarctic and Subantarctic. 87–2,100 m.

Type Species.—*Errina labiata* Moseley, 1879, by original designation (Broch, 1951b).

Inferiolabiata labiata (Moseley, 1879)

Figures 7A–H, 25B, 28I

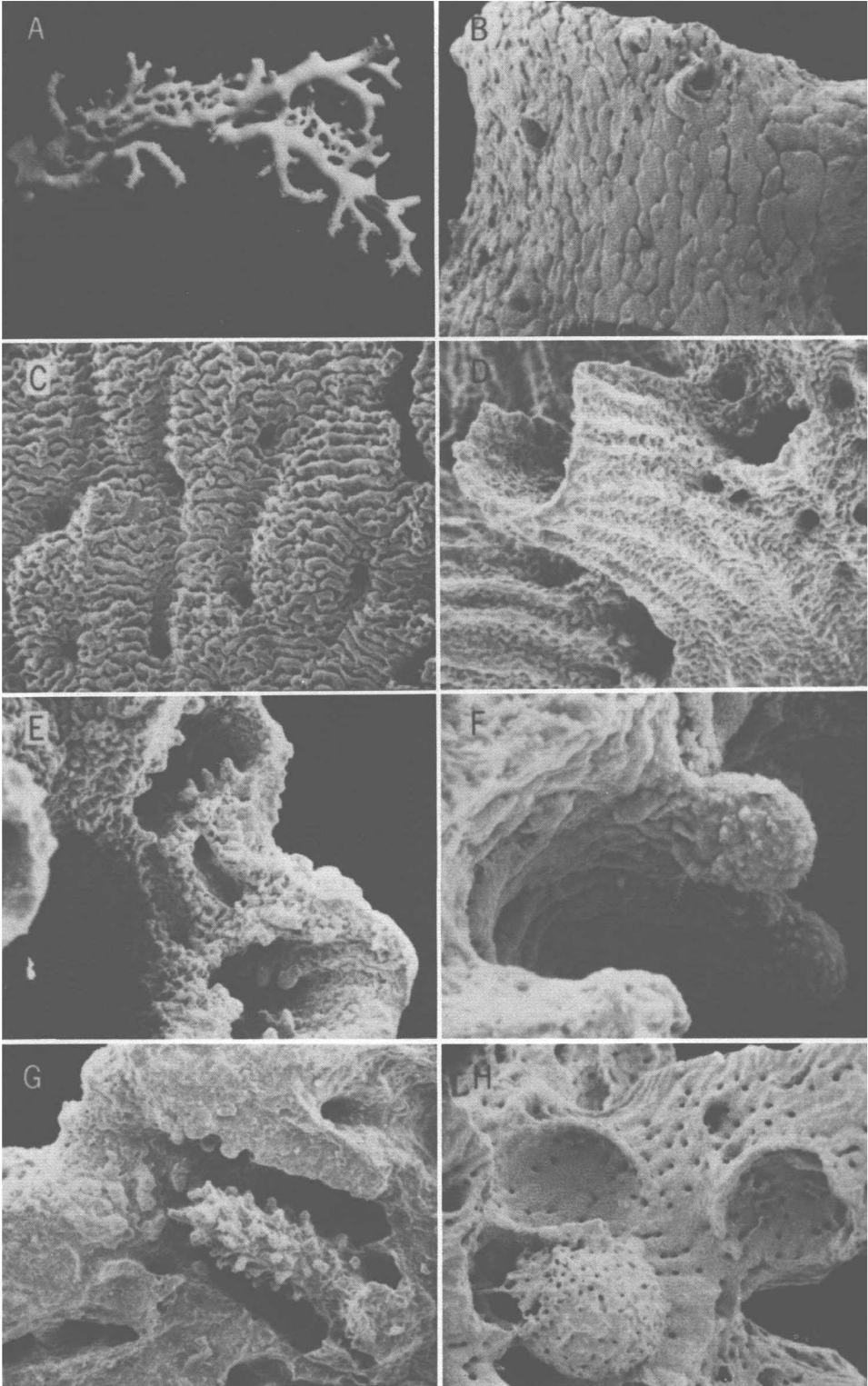
Errina labiata Moseley, 1879: 443–447, pl. 34, fig. 7, pl. 37, pl. 44, figs. 9–11; 1881: 50–55, 80, pl. 1, fig. 7, pl. 4, pl. 11, figs. 9–11 (part: not *Challenger* sta. 135).—Boschma, 1957: 55; 1964e: 287–299, pl. 1; 1966: 109, 117.—Boschma and Lowe, 1969: 15, pl. 5, map 2 (part).

Errina (*Errina*) *labiata*: Hickson, 1912a: 880.

Errina (*Labiata*) *labiata*: Broch, 1942: 39.

Errina (*Inferiolabiata*) *labiata*: Broch, 1951b: 125.—Boschma, 1963a: 337–338.—Cairns, in press: figs. 22D–E, 26A–I, 27A–C.

Diagnosis.—Colony flabellate to bushy; branches highly anastomotic, caused primarily by a symbiotic polychaete worm. Coenosteal reticulation distinct over



entire colony, becoming longitudinal at branch tips. Overall texture at low magnification is porous. Gastropores 0.28–0.33 mm in diameter; gastrostyle up to 1 mm tall, having an H:W of 2.7–6.6. Spines on gastrostyle up to 35 μm tall and 15 μm in diameter. Diffuse ring palisade present. Dactylopore spines up to 0.70 mm tall and 0.23 mm wide, usually laterally fused into tiers of 2–6 spines which encircle part of the branch. Each dactylopore with 1–4 rudimentary dactylostyles, each style composed of 5–10 discrete, cylindrical, blunt pillars up to 50 μm tall and 20 μm in diameter. Ampullae 1.02–1.30 mm in diameter.

Gastrozooids short, squat cylinders with four clavate tentacles. Dactylozooids long and slender, extending far above coenosteal surface. According to Moseley (1881), large nematocysts measuring about $37 \times 15 \mu\text{m}$ occur in nematophores and surface epithelium. Smaller nematocysts measuring $6\text{--}7 \times 3.3\text{--}3.9 \mu\text{m}$ occur abundantly in the dactylozooids. The tube of an exploded nematocyst is about 0.55 μm in diameter and bears a triple spiral of cylindrical spines, each measuring about 0.50 μm long and 0.25 μm in diameter. The spines are directed toward the capsule (Fig. 28I).

Discussion. — This species has been more fully described, discussed, and illustrated by Cairns (in press), and its histology has been well illustrated and discussed by Moseley (1881). Moseley reported two size classes of nematocysts, the larger measuring about $37 \times 15 \mu\text{m}$, the smaller, $16 \times 11 \mu\text{m}$ (from Moseley, 1881: pl. 11, fig. 10). I was unable to find the larger nematocysts in my sections and the smaller nematocysts in many specimens were considerably smaller than Moseley's.

Only one other species is placed in this genus, *I. lowei* Cairns, in press. A comparison of the two species is made in the original description.

Distribution. — Widely distributed in Antarctic and Subantarctic. 87–2,100 m.

Types. — All syntypes deposited at the BM; examined by the author.

Paraerrina Broch, 1942

Paraerrina Broch, 1942: 60–61. — Boschma, 1956: F104.

Diagnosis. — Colonies flabellate; branches round in cross section and blunt tipped; branch anastomosis rare. Coenosteal texture reticulate, covered by small, sharp granules. Gastro- and dactylopores randomly arranged. Gastropores round and flush with surface or very slightly rimmed. Gastrostyles of medium height, not ridged, and bear extremely long, robust, branching spines. Horizontal and vertical tabulae stabilize proximal end of gastrostyle. Dactylopores flush with surface except near branch tips where they are bordered by low dactylopore spines with abcauline slits. Rudimentary dactylostyles present. Ampullae superficial hemispheres, female twice the diameter of male.

Discussion. — At first glance, *Paraerrina* closely resembles *Inferiolabiata* (as previously redefined); in fact, Broch (1942: 61) suggested that the genera may be synonymous. Characters shared by them include: abcauline slit dactylopore spines,

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Figure 7. *Inferiolabiata labiata* (A, Burton Island 592-3: 72°08'S, 172°10'E, 433 m, 13 Jan. 1958; B–C, Eltanin-2021: 73°49'S, 178°13'W, 495–503 m, 15 Jan. 1968; D–H, Eltanin-2092: 76°00'S, 168°49'W, 526 m, 3 Feb. 1968): A, colony with elongate, porous worm tube, $\times 0.62$; B–C, imbricate coenosteal texture, $\times 16$, $\times 80$, respectively; D, ridged dactylopore spines, $\times 70$; E, two dactylopore spines with multiple dactylostyles, $\times 87$; F, dactylostyle elements, $\times 600$; G, gastrostyle and diffuse ring palisade, $\times 87$; H, ruptured and intact ampullae, $\times 17$.

reticulate coenosteal texture, nonridged gastrostyles, rudimentary dactylostyles, and large superficial ampullae. However, *Paraerrina* differs in several significant characters: (1) it has slit dactylopore spines only on distal branch tips, (2) it has only one very rudimentary dactylostyle per dactylopore, (3) its dactylopore spines are well spaced, never clustered, (4) its coenosteal microarchitecture is granular, not imbricate, and (5) its gastrostyle is quite distinctive, with large, branching spines. *Paraerrina* is therefore considered a distinct genus.

Occurrence.—?Oligocene: New Zealand; Recent: known only from off Mauritius. 238–274 m.

Type Species.—*Paraerrina decipiens* Broch, 1942, by monotypy.

Paraerrina decipiens Broch, 1942

Figures 8A–C, 26B

Paraerrina decipiens Broch, 1942: 61–63, 82–83, pl. 5, fig. 19, text-figs. 19, 29.—Boschma, 1956: F104, fig. 84, 2a–b; 1957: 58.

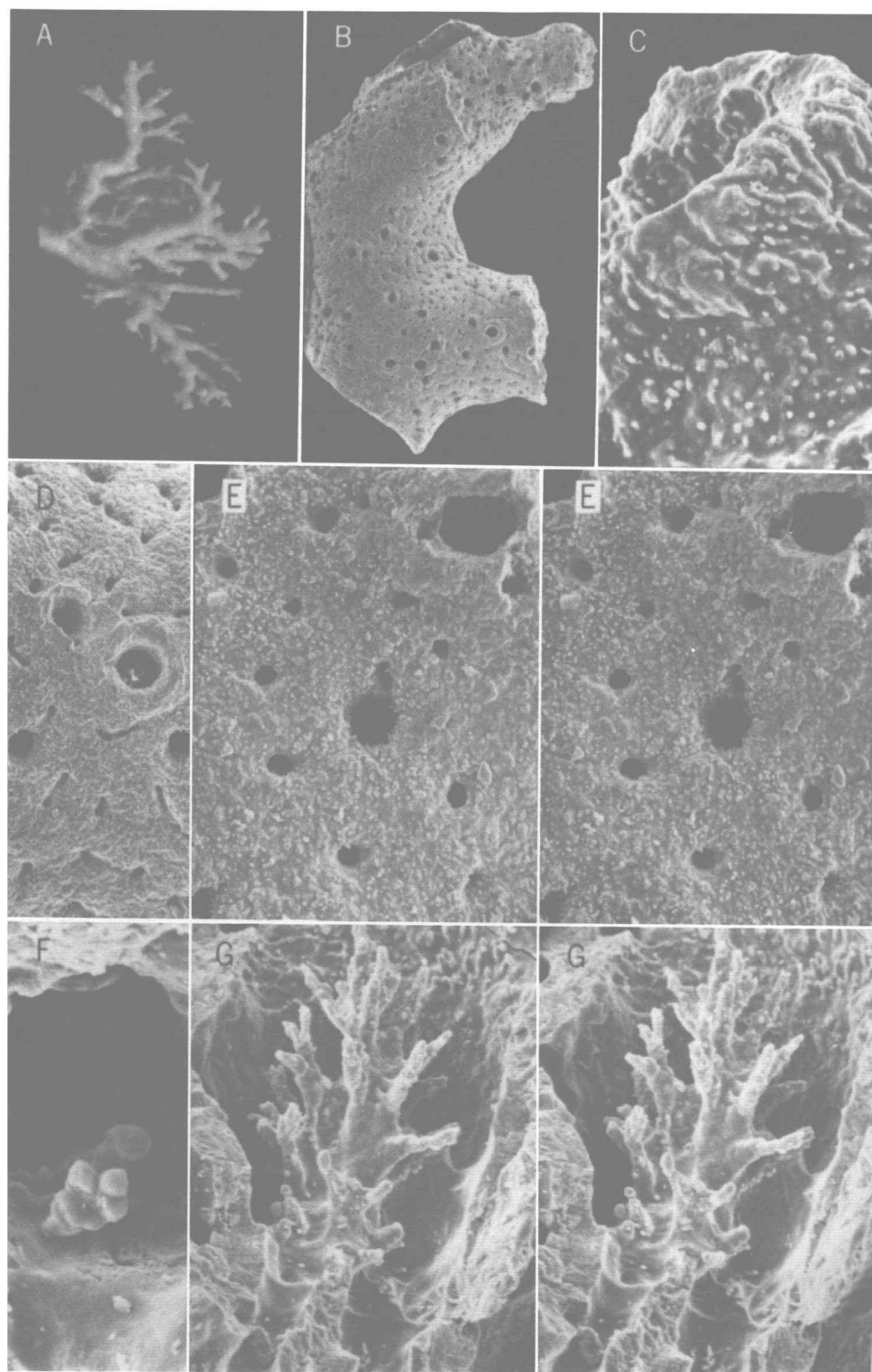
Diagnosis.—Colonies up to 5.5 cm tall and 10 cm broad, with a basal branch diameter up to 9.0 mm. Coenosteal strips 0.13–0.17 mm wide bordered by short, discontinuous grooves about 20 μ m wide and equally deep. These grooves, which are paths of superficial coenosteal canals, terminate in deep pores through which the surface canals communicate with the interior canals. Coenosteum covered by irregularly shaped, pointed granules up to 7.5 μ m tall and 2.5–4.5 μ m in diameter. On the sides of dactylopore spines the granules are elongate, and fuse into vertical ridges up to 40 μ m long. Gastropores 0.12–0.14 mm in diameter. Illustrated gastrostyle 0.25 mm tall, 0.064 mm wide (H:W = 3.9), and bears cylindrical spines up to 75 μ m long and 11 μ m in diameter. Style stabilized by four thick, vertical tabulae and several horizontal tabulae. Dactylopores of same size as gastropores, those on branch tips with a lower lip raised up to 0.12 mm high. Dactylostyle elements up to 26 μ m tall and 9 μ m in diameter. Female ampullae up to 2.0 mm in diameter; male, 0.57–0.69 mm.

Gastrozooids with 0–4 rudimentary tentacles apiece; dactylozooids adnate. One kind of nematocyst, measuring $5.5\text{--}6.5 \times 2.2\text{--}3.0$ μ m, occurs in the coenosteal canals and dactylozooids.

Discussion.—*Paraerrina* is a monotypic genus. It has been reported only twice: the type-specimens of *P. decipiens*, and one fossil fragment from the middle Oligocene of New Zealand identified as *Paraerrina* sp. by Squires (1962). This latter specimen, examined by the author, is similar to *P. decipiens* in branch shape and size, reticulate coenosteal texture, unridged gastrostyle, gastropore tabulae, and superficial ampullae. It differs in having slightly raised, apically perforate gastro- and dactylopores, the latter sometimes linked by low ridges, a condition found in some *Lepidopora*. No grooved dactylopore spines or dactylostyles were present, but this may be the result of the preservation. I share Squires's hesitation in identifying this specimen as belonging to *Paraerrina*, but agree that *Paraerrina* is the most likely choice.

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Figure 8. *Paraerrina decipiens* (A–G, figured syntype from Mauritius, Copenhagen Zoologisk Museum): A, colony, $\times 0.67$; B, branch fragment with gastropores, $\times 11$; C, dactylopore spines on branch tip, $\times 350$; D–E, coenosteal texture and gastropores, $\times 47$, $\times 100$, respectively, E is a stereo pair; F, dactylostyle element, $\times 550$; G, gastrostyle, $\times 215$, stereo pair.



Distribution.—Known only from off Mauritius. 238–274 m.

Types.—The types are deposited at the Zoologisk Museum, Copenhagen. The figured syntype was examined by the author. The type-specimens are heavily infested by boring barnacles (*Lithoglyptes* fide Broch, 1942), which produce large slits about 1.5 mm long and 0.5 mm wide along the lateral branch edges.

Stellapora new genus

Acanthopora Moseley, 1876b: 94 (name preoccupied by Orbigny, 1849).

Spinipora Moseley, 1879: 447, 476; 1881: 55 (name preoccupied by Agassiz, 1846).

Errina (*Spinipora*): Hickson, 1912a: 881.—Broch, 1942: 39.

Errina (*Inferiolabiata*): Boschma, 1956: F102 (part); 1963a: 338 (part); 1964e: 294 (part).

Errina: Boschma, 1957: 53 (part).

Diagnosis.—Colonies robust, flabellate to slightly bushy; branches thick, anastomotic, and bluntly tipped. Coenosteal texture reticulate, covered by irregularly shaped granules. Gastro- and dactylopores randomly distributed over coenosteum. Gastropores large, round, or stellate in shape. Gastrostyle slender with longitudinal ridges and a pointed tip; fused spines ornament the ridges. No ring palisades. Dactylopore spines are dimorphic: the larger spines are very tall, thin-walled, and spout-like with an abruptly truncated tip. They are grooved along the side facing the top of the colony (abcauline) and are not ridged on their lower sides. They often cluster together and some appear to be composite. The smaller dactylopore spines are small, raised, elliptical slits or apically perforated mounds. No dactylostyles. Ampullae superficial, hemispherical.

Discussion.—The single species referred to *Stellapora*, *S. echinata* (Moseley, 1879), was placed by Moseley in a separate genus, *Spinipora*, which he considered to be "closely allied to *Errina*." Hickson (1912a) maintained *Spinipora* as a discrete, monotypic taxon but as a subgenus of *Errina*, and Boschma (1956; 1963a) finally merged it with the subgenus *Inferiolabiata*, which arbitrarily combined all *Errina* that have abcauline grooved dactylopore spines. In my opinion, Moseley was correct in placing *S. echinata* in a separate genus because of its significant morphological differences from *Inferiolabiata*, i.e., reticulate-granular coenosteal texture (vs. reticulate-imbricate), stellate gastropores (vs. round), ridged gastrostyles with fused spines (vs. cylindrical gastrostyles with individual spines), and dimorphic, nonridged dactylopore spines without dactylostyles (vs. monomorphic, ridged dactylopore spines with 1–4 dactylostyles apiece). *Stellapora* differs from *Lepidotheca* in the same characters as well as being much more robust and having much better developed dactylopore spines. The character of stellate gastropores is unique to *Stellapora*.

Both of Moseley's generic names are preoccupied and the type-species of *Inferiolabiata* is *I. labiata*, a separate genus, making it necessary to establish a new generic name for *S. echinata*.

Etymology.—The generic name refers to the stellate appearance of some of the gastropores of *S. echinata*. Gender: feminine.

Occurrence.—Recent: Southwest Atlantic. 357–1,647 m.

Type Species.—*Spinipora echinata* Moseley, 1879.

Stellapora echinata (Moseley, 1879)

Figures 9A–I, 251

Spinipora echinata Moseley, 1879: 447–449, pl. 34, fig. 3, pl. 35, fig. 4, pl. 38; 1881: 55–57, pl. 1, fig. 3, pl. 2, fig. 4, pl. 5.

Errina (*Spinipora*) *echinata*: Hickson 1912a: 881, pl. 95, fig. 8.

Not *Spinipora echinata*: Hickson and England, 1909: 352, pl. 44, fig. 8.

Errina echinata: Boschma, 1957: 53.—Boschma and Lowe, 1969: 15, pl. 5, map 2.

Errina (*Inferiolabiata*) *echinata*: Boschma, 1963a: 338; 1964e: 293–294, 298.—Cairns, in press: figs. 22B–C, 24A–H, 25A–B.

Diagnosis.—Colonies up to 23 cm tall with a basal branch diameter of 2.5 cm; distal branches round in cross section, 2.5–5.0 mm in diameter. Coenosteal strips 0.16–0.22 mm wide, covered by irregularly shaped granules 5–10 μ m in diameter. Gastropores abundant and large (0.41–0.68 mm in diameter); each stellate pore has 1–7 grooves along its inner edge, which produce a stellate pattern at the surface not unlike a cyclostyle. Gastrostyles up to 0.9 mm tall with an H:W around 4–5. Large dactylopore spines are up to 2.5 mm tall and 0.55 mm wide; smaller spines with pore diameters of 0.12–0.20 mm. Ampullae 1.1–1.3 mm in diameter, often ruptured.

Gastrozooids long and cylindrical, each with six long tentacles. Larger dactylozooids adnate, composed of an elongate base which lies along the dactylopore spine and a short, free part near the end of the base (see Moseley, 1881: pl. 5). Smaller dactylozooids simple, basally attached. Nematocysts common in dactylozooids and coenosteal canals, measuring $11.0\text{--}11.5 \times 4.5\text{--}5.0 \mu\text{m}$.

Discussion.—*Stellapora* is a monotypic genus. It has been more fully described and discussed by Cairns (in press) as *E. (I.) echinata*.

Distribution.—Known only from off Uruguay and off Burdwood Bank. 357–1,647 m.

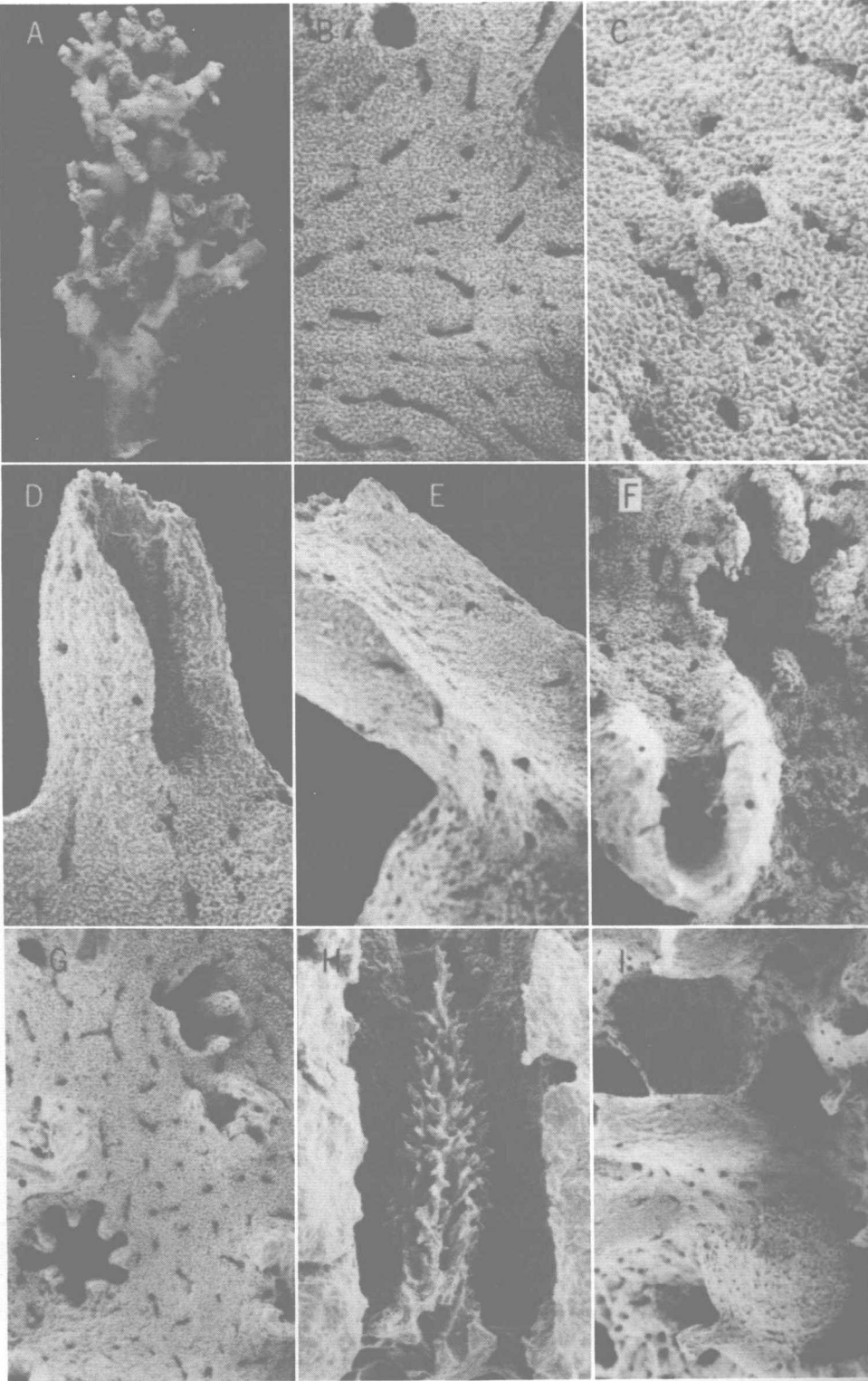
Types.—The holotype is deposited at the BM (1880.11.25.174, 196); examined by the author.

Errinopsis Broch, 1951

Errinopsis Broch, 1951a: 40.—Boschma, 1956: F104, fig. 85, 4.

Diagnosis.—Colonies uniplanar, sometimes with accessory flabella projecting perpendicular to main flabellum. Colony secondarily attached to substrate by numerous, relatively slender branches. Branching highly anastomotic, producing fenestrate flabella. Branches elliptical to rectangular in cross section, the greater axis of the branch oriented perpendicular to the flabellum; ratio of branch edges as high as 1:4. Coenosteal texture reticulate to slightly linear, covered by low, rounded granules; however, some dactylopore spines are coarsely imbricate. Gastro- and dactylopores occur on all branch surfaces but tend to concentrate on anterior and anterolateral edges. Gastrostyles lanceolate, attaining their greatest width at their midpoints; H:W ratio medium. Styles ridged, the ridges bearing fused spines; no ring palisades or tabulae. Dactylopore spines of two kinds: (1) low, apically perforate mounds, and (2) tall, thick, adcauline-grooved tubercles. The tall dactylopore spines sometimes add one or more extensions apically which serve as the forerunner of branch anastomosis. They may also have additional dactylopores producing large, usually bifurcate, composite spines. No dactylostyles. Ampullae superficial and irregular in shape, sometimes with a lateral tubular efferent duct.

Discussion.—*Errinopsis* appears to be morphologically intermediate between the more primitive genera with apically perforate dactylopores, such as *Lepidopora*, and the more advanced errinine genera that have coordinated, thick-walled, grooved dactylopore spines, such as *Errina*, *Errinopora*, and *Gyropora*. It is similar to *Lepidopora* in having randomly arranged gastro- and dactylopores and apically



perforate dactylopores, but more advanced in having ridged gastrostyles and thick-walled, adcauline-grooved dactylopore spines. It differs from the other group of errinine genera (*Paraerrina*, *Inferiolabiata*, *Lepidotheca*, *Stellapora*, and *Phalangopora*) in having differently shaped and oriented dactylopore spines and a different coenosteal texture (reticulate-granular vs. predominantly imbricate).

Occurrence.—Recent: Off southern tip of South America. 250–771 m.

Type Species.—*E. reticulum* Broch, 1951, by original designation.

Errinopsis reticulum Broch, 1951
Figures 10A–H, 27C

Errinopsis reticulum Broch, 1951a: 37–41, pl. 2, fig. 2, pl. 3, figs. 1–2, text-figs. 3–7.—Boschma, 1956: F104, fig. 85, 4; 1957: 59; 1966: 117.—Boschma and Lowe, 1969: 15, pl. 5, map 4.—Cairns, in press: figs. 1G–H, 9A–H.

Diagnosis.—Colonies up to 25 cm tall and 35 cm broad; fenestrae rarely larger than 2–3 square mm. Coenosteal strips about 50 μ m wide covered by rounded granules 6–8 μ m in diameter; coenosteum orange to pink. Gastropores round, 0.15–0.30 mm in diameter, and flush with the surface. Styles up to 0.60 mm tall; H:W ranges from 3.3–3.9. Small, apically perforate dactylopores 45–70 μ m in diameter, about 25 μ m tall. The less numerous, grooved dactylopore spines are between 0.20–0.30 mm in diameter and up to 1.7 mm tall (including apical extensions), having grooves 40–60 μ m wide. Ampullae 0.65–0.77 mm in diameter.

Gastrozooids have 4–6 short tentacles. Dactylozooids both simple and adnate. Rod-shaped nematocysts measuring 8.6–11.1 \times 2.3–3.1 μ m and more spherical ones measuring 10.5–12.0 \times 4.0–4.5 μ m occur in coenosteal canals, dactylozooids, and in the ectoderm, oriented perpendicular to the surface. Male ampullae may contain 2–4 gonophores, female ampullae usually have but one.

Discussion.—Broch (1951a: 40) stated that *E. reticulum* has only one kind of dactylopore spine, hypothesizing that the large, grooved spines grew from the low, apically perforate ones. Although he stated that he was able to find many intermediate forms bridging the differences between the simple and spiniferous pores, I do not find these intermediate forms by examination of either the skeleton or the dactylozooids. At least two kinds of dactylozooids (and dactylopore spines) occur, of which the medium-sized, grooved spines (Fig. 10G) are very similar to those of *Errina*. Broch also stated that only simple dactylozooids are present, but adnate dactylozooids occur in the tall dactylopore spines.

Only one other species is known in this genus, *E. fenestrata* Cairns, in press; comparisons to *E. reticulum* are made by Cairns (in press).

Distribution.—Known only from area bounded by Tierra del Fuego, Burdwood Bank, and Falkland Islands. 250–771 m.

Types.—Broch (1951a) designated two allotypic syntypes from the four colonies he examined. Their deposition is unknown.

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Figure 9. *Stellapora echinata* (A–I, Eltanin-1593: 54°43'S, 56°37'W, 339–357 m, 14 Mar. 1966): A, colony, $\times 0.27$; B, coenosteal texture, $\times 40$; C, dactylopore, $\times 75$; D–E, dactylopore spines, $\times 47$, $\times 40$, respectively; F, dactylopore spine from above and stellate gastropore, $\times 40$; G, stellate gastropores, $\times 27$; H, gastrostyle, $\times 60$; I, dactylopore spines and an ampulla, $\times 20$.

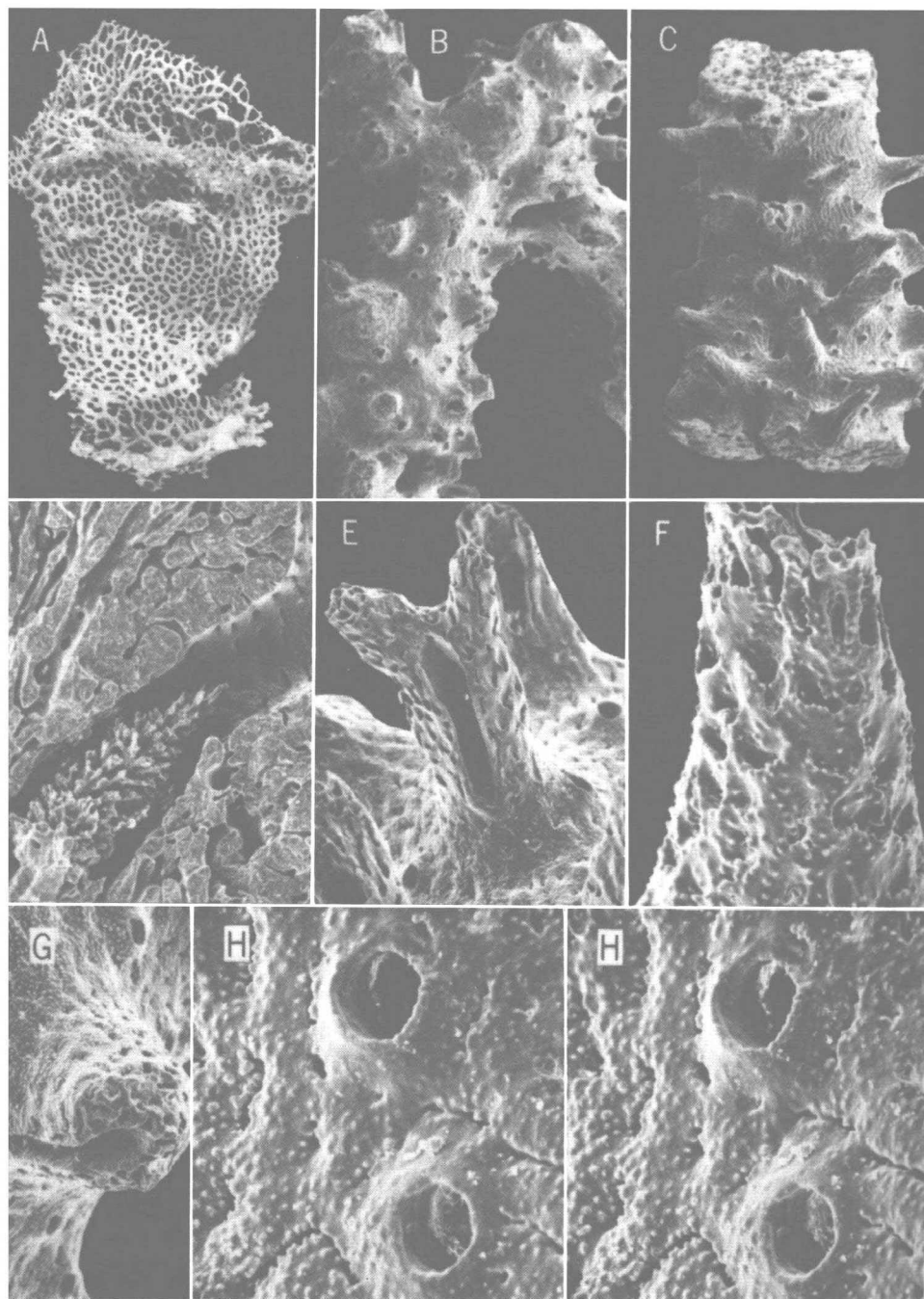


Figure 10. *Errinopsis reticulum* (A, Walther Herwig 19/76: 54°49'S, 57°52'W, 230–250 m, 27 Nov. 1975; B, D, Hero 715–895: 55°00'S, 64°50'W, 438–548 m, 3 Nov. 1971; C, E–H, Hero 715–879: 54°50'S, 63°50'W, 342–353 m, 28 Oct. 1971): A, large colony, $\times 0.27$; B, branch fragment with gastropores, both types of dactylopores, and ampullae, $\times 15$; C, branch fragment with gastropore and both types of dactylopores, $\times 14$; D, gastrostyle, $\times 57$; E–G, dactylopore spines, $\times 53$, $\times 150$, $\times 77$, respectively; H, two conical, apically perforate dactylopores, $\times 175$, stereo pair.

Errina Gray, 1835

Millepora: Linnaeus, 1767: 1282 (part).

Madrepora: Müller, 1775: 715 (part).

Errina Gray, 1835: 85.—Cairns, in press.

Porella: Gray, 1872: 482.

Labiopora Moseley, 1879: 476.

Errina (*Labiopora*): Hickson, 1912a: 879, 881.

Errina (*Eu-Errina*) Broch, 1942: 38.

Errina (*Errina*): Boschma, 1956: F102, figs. 83, 1a–b; 1963a: 337; 1964d: 284; 1965b: 21.

Diagnosis.—Colonies usually flabellate but may be slightly bushy; branches robust to delicate, usually round in cross section, may or may not anastomose. Coenosteal texture usually reticulate with irregularly shaped granules, but may be linear and have low, rounded granules; the sides of dactylopore spines are sometimes imbricate. Coenosteum white, orange, or pink. Gastro- and dactylopores usually randomly arranged on branch; however, gastropores often more abundant on anterior side, and sometimes seem to be aligned along the anterior or lateral branch edges. Gastropores may or may not bear an abcauline lip. Gastrostyles usually of medium H:W; however, they range from 1.6–26, the longer styles held in place by transverse tabulae. Styles lanceolate, usually vertically ridged, the ridges bearing simple and fused spines; a ring palisade is present in some species. Dactylopore spines shaped as grooved tubercles, the grooves predominantly directed away from the branch tip (adcauline). Walls of the dactylopore spines usually thick, such that the groove constitutes only one-third the width of the spine. Spines vary greatly in size from rudimentary to over 1 mm tall; small dactylopores also occur as slits, flush with the branch surface. Spines are often clustered and sometimes composite. No dactylostyles. Ampullae vary from internal to slightly submerged to fully superficial hemispheres.

Discussion.—*Errina* is similar to *Errinopsis*, differing primarily in having either grooved dactylopore spines or dactylopores flush with the surface, not apically perforate conical or composite dactylopores. *Errina* also has more openly branched colonies and cylindrical branches (vs. rectangular in cross section).

Occurrence.—Paleocene: Denmark; Recent: North Atlantic, off South Africa, ? off Mauritius, New Zealand Region, Subantarctic and Antarctic. 6–1,772 m.

Errina has been reported from Mauritius as *E. aspera mascarina* by Boschma (1965a); however, Zibrowius strongly doubts this distributional record, implying that this specimen probably was collected in the Mediterranean (personal communication, 1981).

Type Species.—*Millepora aspera* Linnaeus, 1767, by monotypy.

Errina aspera (Linnaeus, 1767)

Figure 11A–G

Millepora aspera Linnaeus, 1767: 1282–1283.

Madrepora aspera: Müller, 1775: 715.

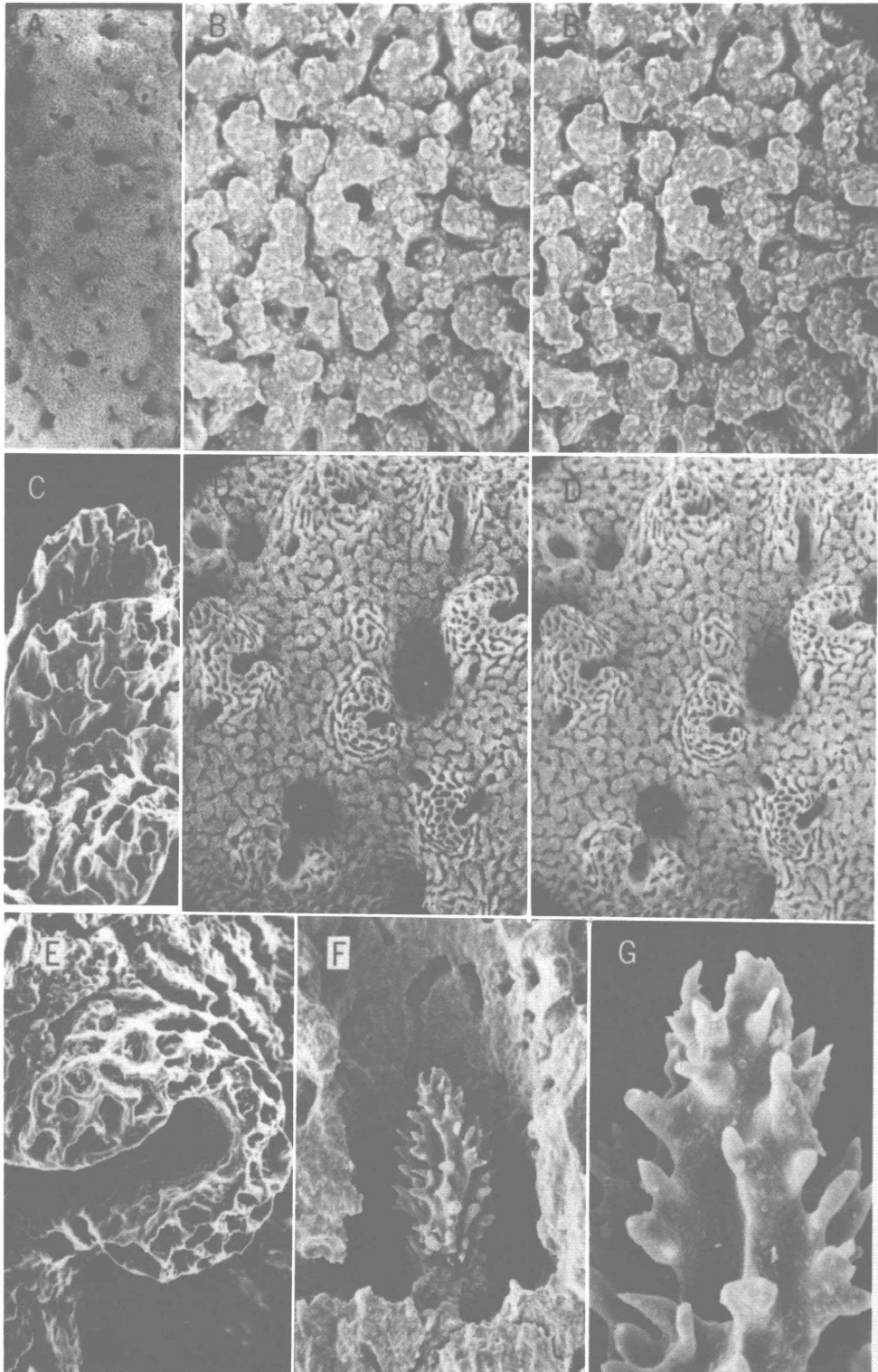
Errina aspera: Gray, 1835: 85.—Not Verrill, 1864: 46 (= *E. dabneyi*).—Not Pourtalès, 1867: 116 (= *E. dabneyi*).—Boschma, 1953a: 301–310, figs. 1–5; 1953b: 311–314; 1953c: 32–34; 1954: 143–149, pls. 1–3, text-fig. 1; 1957: 50–51; 1965a: 1–6, pl. 1, figs. 5–7, text-fig. 2.—Not Boschma and Lowe, 1969: 15 (= *E. gracilis*).

Errina (*Labiopora*) *aspera*: Hickson, 1912a: 888–889, pl. 95, fig. 6; ?1912b: 462.

?*Errina dabneyi*: Hickson, 1912b: 463–464, pl. 8, lower fig.

Errina (*Eu-Errina*) *aspera*: Broch, 1942: 38 (not pp. 40–42).

Errina (*Errina*) *aspera*: Boschma, 1956: F100; 1963a: 337.



Diagnosis.—Colonies predominantly flabellate with only a few branches out of the plane of the fan. Branches of moderate diameter; no branch anastomosis. Coenosteal texture reticulate: strips about $45\ \mu\text{m}$ wide, bordered by broad, shallow grooves. Strips covered by irregularly shaped granules, the texture changing to fused imbricated platelets on the sides of dactylopore spines. Coenosteum white. Gastropores round, $0.15\text{--}0.20\ \text{mm}$ in diameter, without lower lip. Gastrostyles lanceolate, $0.19\text{--}0.27\ \text{mm}$ tall with an $H:W = 1.5\text{--}3.1$. Style ridged, the ridges bearing simple and fused spines. No supporting tabulae or ring palisades. Dactylopore spines up to $0.50\ \text{mm}$ tall and $0.25\ \text{mm}$ wide; adcauline groove about $50\text{--}60\ \mu\text{m}$ wide or one-fourth to one-third the width of the spine. Dactylopore spines sometimes clustered. Some dactylopores are flush with the surface and measure about $160 \times 60\ \mu\text{m}$. Ampullae partially submerged in branch, $0.35\text{--}0.70\ \text{mm}$ in diameter. Soft parts unknown.

Discussion.—Soft parts of *E. aspera* were not available for study, but tissue of the closely related species *E. antarctica* was studied by Broch (1942; 1951a). He observed that the gastrozooids have 3–6 tentacles, usually 4. The dactylozooids are dimorphic: the smaller ones corresponding to flush dactylopores are simple, whereas those corresponding to grooved dactylopore spines are adnate (Fig. 25C). Three to six male gonophores and one female gonophore occur per ampulla (Fig. 26G). The spadix is highly branched. To this I can add that rod-shaped nematocysts, measuring $12.0\text{--}13.5 \times 3.0\text{--}3.3\ \mu\text{m}$, are common in the coenosteal canals, dactylozooids, and ectoderm.

Sixteen species are attributed to *Errina* (Table 1). Representative specimens—usually the types—have been examined of all but two of these species. Additional species are likely to be described from the New Zealand region by the elevation of some of the four “facies” of *E. novaezealandiae*, and the description of new species by Zibrowius (personal communication, 1981).

The fossil species *E. irregularis* Nielsen, 1919 is herein transferred from *Errina* (*Inferiolabiata*) to *Errina* s.s., as Boschma (1964e: 294) thought might be the case. Examination of the types reveals typical clustered *Errina*-type dactylopore spines with adcauline grooves and a reticulate coenosteal texture.

Another species, *E. macrogastrea* Marenzeller, 1904, from the Galapagos, has, in the past, been tentatively assigned to *Errina* s.s. Both Hickson (1912a) and Broch (1942) recognized that this species has the dactylopore spines of *Errina* s.s. but the coenosteum of *Inferiolabiata* (*Lepidotheca* in this paper). Boschma (1964d: 285), giving less importance to coenosteal texture, assigned it to *Errina* s.s. In my opinion, *E. macrogastrea* remains an enigma, having linear-imbricate coenosteal texture (like all *Lepidotheca*, not like *Errina* s.s.) but adcauline grooved dactylopore spines (like all *Errina*, not like *Lepidotheca*). As Broch (1942: 39) stated, it holds a perplexing intermediate position between the two genera.

New Records.—CALYPSO, $6^{\circ}00'W$, $33^{\circ}54'N$, 110 m, 30 Aug. 1958, USNM 59931 and SME 1282.

Distribution.—Mediterranean Sea, off Morocco, ? off Cape Verde Islands. ?–110 m—? *E. aspera* is the only stylasterine known from the Mediterranean (Boschma, 1965a).

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Figure 11. *Errina aspera* (A–G, Calypso-“1282”: $33^{\circ}54'N$, $6^{\circ}00'W$, 110 m, 30 Aug. 1958): A, branch segment showing gastro- and dactylopores, $\times 10$; B, reticulate coenosteal texture, $\times 133$, stereo pair; C, E, dactylopore spines, $\times 113$, $\times 133$, respectively; D, gastropores and dactylopore spines, $\times 36$, stereo pair; F–G, gastrostyle, $\times 133$, $\times 465$, respectively.

Types.—Deposition unknown; probably lost.

Errinopora Fisher, 1931

Errina: Dall, 1884: 470 (part).

Errinopora Fisher, 1931: 397; 1938: 536.—Boschma, 1956: F102.

Protoerrina Broch, 1935: 59; 1936: 99–100.

Diagnosis.—Colonies uniplanar to slightly bushy, sometimes attached by a broad encrusting base. Branches round, elliptical, or platelike in cross section; usually robust with blunt or clavate tips; branch anastomosis sometimes occurs. Coenosteal texture reticulate to spongy, covered by round to irregularly shaped granules; coenosteum orange, yellow, pink, or white. Gastropores arranged in irregular vertical rows, short horizontal terraces, or randomly; no gastropore lips. Gastrostyles of medium H:W, bearing vertical or oblique ridges. Ridges bear tall, cylindrical, clavate spines, some of which are bifurcate. Gastropores do not have tabulae or ring palisades. Dactylopore spines robust, like those of *Errina* s.s., often fused laterally, forming chains flanking one or both sides of a line of gastropores, their grooves directed toward the pores. Often, towards the base of a colony, several dactylopores are positioned around an isolated gastropore, so as to closely resemble a cyclosystem. Sometimes there is no coordination of gastro- and dactylopores, the dactylopore spine grooves being uniformly abcauline. Dactylostyles well developed, expressed as a spiny ridge extending most of the length of the dactylopore spine. Ampullae superficial, sometimes clustered, and usually quite large; hemispherical or conical.

Discussion.—*Errinopora* represents an advance over *Errina* in two major features: the presence of a well-developed dactylostyle and a higher degree of gastro- and dactylopore coordination. A progression of this increased coordination is seen within the genus: the dactylopore spines of *E. nanneca* are primarily abcauline, slightly terraced but usually individualized, with little coordination with the gastropore; the dactylopore spines of *E. zarhyncha* are often fused and terraced but only on one side of a gastropore row; the dactylopore spines of *E. cestoporina* and *E. lobata* are terraced beneath rows of gastropores and have some reduced, adcauline dactylopore spines distal to the gastropores; finally, the dactylopore spines of *E. pourtalesii*, *E. stylifera*, and *E. latifundata* form fused terraces on both sides of gastropore rows and, on basal branches, rings of dactylopore spines encircle isolated gastropores, forming pseudocyclosystems. It is this last character that led Broch (1936) to place *Protoerrina* (= *Errinopora*) in the Stylasterinae. Because of the similarities of *Protoerrina* with *Errina* and *Distichopora*, Broch (1936) went on to suggest that it was a primitive genus, and that the Stylasterinae was the most primitive of the subfamilies. However, I agree with Boschma (1960: 432–433) that the pseudocyclosystems of *Errinopora* are not primitive but a result of ontogenetic reduction, the typical condition revealed at the branch tips, i.e., meandering rows of gastro- and dactylopores. I would therefore place *Errinopora* as the most advanced genus of Errininae (with the possible exception of *Gyropora*), with close affinities to *Stylaster* (Group A), forming a transition between these two subfamilies.

Occurrence.—? Paleocene: Denmark; Recent: North Pacific, off Tierra del Fuego. 49–518 m.

Type Species.—*Errina pourtalesii* Dall, 1884, by original designation.

Errinopora pourtalesii (Dall, 1884)

Figures 12A–I, 24I, 25K, 28D

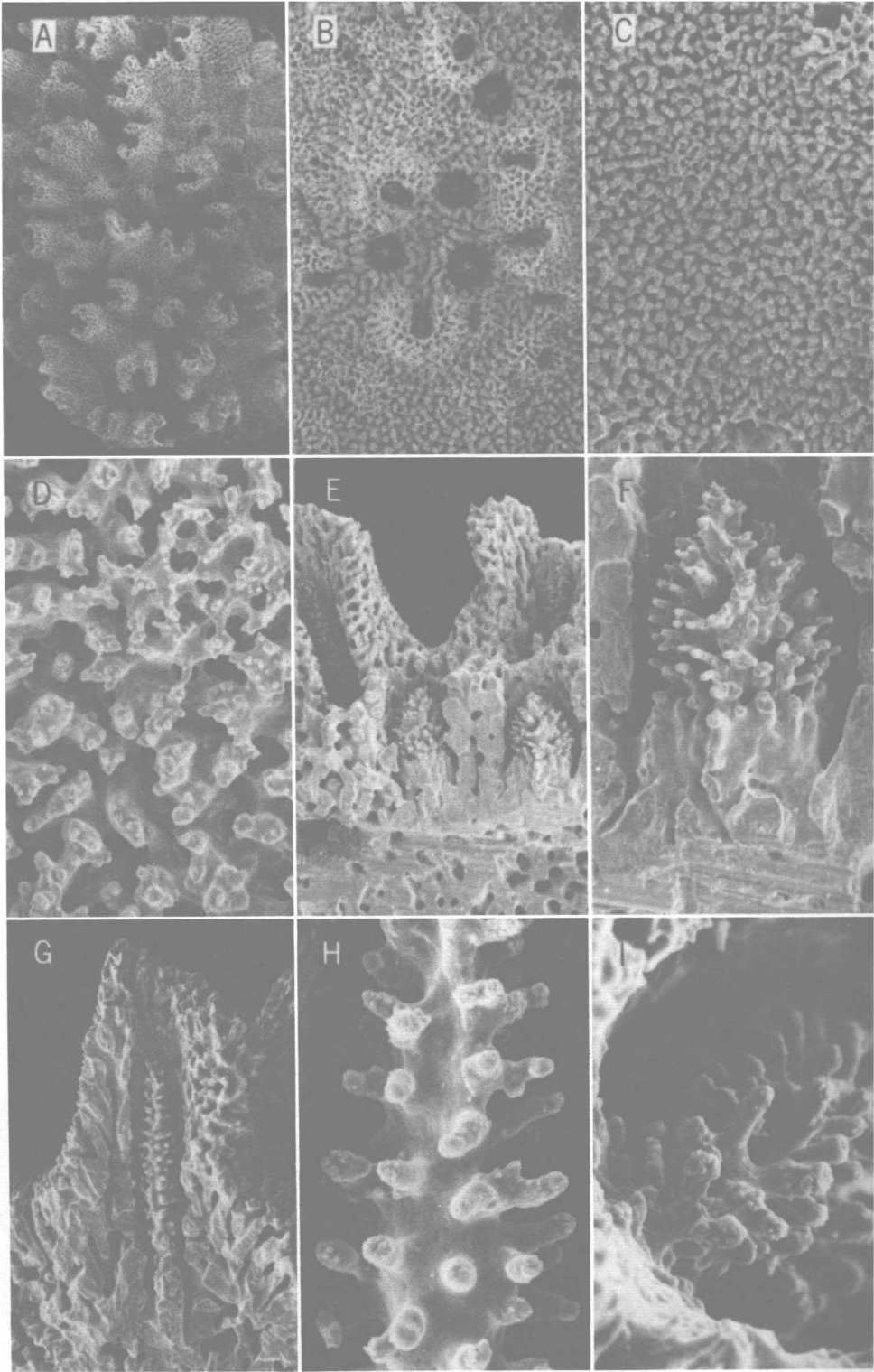
Errina pourtalesii Dall, 1884: 114–115.*Errinopora pourtalesii*: Fisher, 1931: 397–398, pl. 16, fig. 4, pl. 17, fig. 7; 1938: 541–542, pl. 65, fig. 2, pl. 66, fig. 2, pl. 70, fig. 1.—Boschma, 1956: F104; 1957: 58; 1960: 428–430.—Lowenstam, 1964: 382–383.

Diagnosis.—Colonies flabellate to slightly bushy, up to 18 cm tall and 26.5 cm broad, firmly attached by a broad encrusting base. Branches robust and round in cross section with blunt or slightly clavate branch tips; anastomosis rare. Distal branches 4–6 mm in diameter, basal branch diameters up to 1.5 cm. Coenosteum very similar to that of *Sporadopora dichotoma*: reticulate-granular, but very porous, with very short strips bordered by broad, deep channels. Coenosteum pinkish orange, except at branch tips and leading edges of basal encrustation, which are white. Gastropores round, 0.20–0.35 mm in diameter, flush with the surface. Gastropores arranged in irregular vertical to oblique rows of 5–20 pores near branch tips, becoming isolated into shorter rows or single pores toward the base. Illustrated gastrostyle 0.32 mm tall, 0.15 mm broad (H:W = 2.1) with broad, diagonal ridges. Spines on gastrostyle up to 39 μ m tall and 9–10 μ m in diameter, each terminating in a crown of several dozen small tufts, each tuft about 1.6 μ m in diameter. Dactylopore spines often fused laterally, their grooves invariably pointing toward the closest gastropore, resulting in long chains of dactylopore spines flanking a row of gastropores or, toward the base, 4–5 spines surrounding one or two gastropores: a pseudocyclosystem. Dactylopore spines up to 1.2 mm tall and 0.37–0.46 mm broad, the groove about 0.14 mm wide. Exterior of spines vertically ridged, the ridges about 20 μ m wide and separated by broad, shallow grooves also about 20 μ m wide. Inside each dactylopore spine there is another ridge opposite the slit, the dactylostyle, measuring about 60 μ m tall and 60 μ m broad, up to 0.67 mm long, bearing spines similar to those of the gastrostyle: 30 μ m tall, 10 μ m in diameter, with a tufted, clavate tip. Ampullae very spongy, about 0.50 mm in diameter.

Gastrozooids tentacles very small. Dactylozooids adnate, the free part overhanging an adjacent gastrozooid. Large nematocysts, 12.5–14.0 \times 4.1–5.0 μ m, are common in the ectoderm, especially the tissue of the dactylopore spines and around each gastropore. The dactylo- and gastrozooid tentacles bear smaller nematocysts measuring 7.0 \times 3.0–3.5 μ m. Another type, 10.0 \times 2.7 μ m, is rare in coenosteal canals. Gonophores not examined.

Discussion.—Six species are assigned to the genus *Errinopora* (Table 1) and another two, *Labiopora lobata* Nielsen, 1919 and *Errina porifera* Naumov, 1960, are tentatively assigned to the genus. *L. lobata* has a reticulate coenosteum and dactylopore spines arranged similar to those of *E. cestoporina*; unfortunately, few other characters are adequately preserved (e.g., the dactylostyle), making a confident generic placement unlikely. Specimens of *Errina porifera* were not examined; however, Naumov's description also indicates a dactylopore spine arrangement similar to that of *E. cestoporina*. But, without examining the type, it is impossible to rule out a placement in *Inferiolabiata* or even *Lepidopora* for *E. porifera*.

Errinopora intervacans Naumov, 1960, is herein synonymized with *E. styliifera*. The character used by Naumov to distinguish *E. intervacans* from other species—its hollow branches—is the result of a clonid sponge excavation (personal communication, K. Ruetzler, 1982). It is otherwise similar to *E. styliifera*.



The specimen described by Naumov (1960: 555) as *Errina antarctica* is an *Errinopora*, also very similar to *E. styliifera*.

Finally, the taxonomic position of "*Errina*" *cyclopore* Cairns, in press, is problematic. It has the gastro-dactylopore coordination and coenosteal texture of *Errinopora cestoporina* but differs primarily in lacking dactylostyles. *E. cyclopore* probably represents either an offshoot from *Errinopora*, involving the loss of dactylostyles, or occupies a transitional position between *Errina* and *Errinopora* before dactylostyles had developed.

Remarks.—*E. pourtalesii* is often infested with a spionid polychaete, which forms a U-shaped tube, each arm of which is closely adjacent and measures about 1 mm in diameter. Boring bivalves and barnacles also live within the coenosteum of this hydrocoral, both producing prominent galls.

New Records.—ALBATROSS-3160, 37°48'35"N, 123°12'40"W, 71 m, USNM 52254.

Distribution.—Known only from off central California. 49–183 m.

Types.—A small fragment (syntype) bearing the number 6853 is deposited at the USNM. Presumably the larger colony is at the MCZ. The former was examined. Representatives, usually types, of all of the species mentioned in the discussion, except *E. porifera*, have been examined by the author.

Gyropora Boschma, 1960

Gyropora Boschma, 1960: 423.

Diagnosis.—Colonies flabellate and sparsely branched; small colonies columnar. Branches thick, round to elliptical in cross section, and blunt. Coenosteum reticulate-granular and pale reddish purple. Gastropores linearly arranged in sunken, meandering, and bifurcating valleys up to 30–40 pores long; shorter valleys and isolated pores also occur. Gastrostyles longitudinally ridged and prominently spinose, of medium H:W. Dactylopore spines similar to those of *Errina* s.s. and *Errinopora* in construction; however, the spines are fused laterally, often having common walls between them. Grooves of spines always directed toward gastropores, forming a low, continuous perimeter on each side of a gastropore valley. A ring of dactylopore spines encircles isolated gastropores, producing pseudocyclosystems. No dactylostyles. Ampullae not observed.

Discussion.—*Gyropora* is considerably more advanced than *Errina* in regard to its gastro-dactylopore coordination. It is similar to *Errinopora* in its gastrostyle structure and dactylopore spine orientation, but is more specialized in having sunken rows of gastropores, reduced dactylopore spines, and, in most cases, common dactylopore spine walls; *Gyropora* also differs in lacking dactylostyles. I agree with Boschma's (1960) placement of *Gyropora* in the Errininae. In my opinion, it is the most specialized genus in the subfamily (because of its highly coordinated gastro- and dactylopores) but probably represents an evolutionary cul-de-sac; the closely related *Errinopora* seems to be the transition between the Errininae and Stylasterinae.

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Figure 12. *Errinopora pourtalesii* (A, E–I, Albatross-3160: 37°49'N, 123°13'W, 71 m, 22 Mar. 1890; B–D, Albatross-3159: 37°47'N, 123°10'W, 49 m, 22 Mar. 1890): A, branch segment, ×12; B, a short pore row near base of colony, ×23; C–D, coenosteal texture, ×33, ×133, respectively; E, branch cross section revealing gastro- and dactylostyles, ×40; F, gastrostyle, ×133; G–I, dactylostyle, ×50, ×350, ×430, respectively.

Occurrence.—Known only from off Cape Agulhas, South Africa. 22 m.

Type Species.—*Gyropora africana* Boschma, 1960, by original designation.

Gyropora africana Boschma, 1960

Figures 13A–H, 24J, 25L

Gyropora africana Boschma, 1960: 423–433, pl. 1, figs. 1–9, text-fig. 1a–d.—Vervoort and Zibrowius, 1981: 26–27.

Diagnosis.—Colonies up to 2.9 cm tall and 2.7 cm broad; terminal branches $5.5-6.5 \times 4.0-4.5$ mm in diameter, basal branch up to 13.5 mm in greater diameter. Coenosteal strips 0.10–0.11 mm wide, flat to slightly convex, and separated by deep slits about 15–20 μ m wide. Gastropores round, 0.20–0.41 mm in diameter, linearly arranged in meandering valleys sunken about 0.7 mm below the coenosteal surface. Toward the branch tips the valleys sometimes anastomose, forming irregularly shaped “islands” of coenosteum. Toward the base of colonies the space between valleys is much broader and the valleys shorter, with less branching. Gastrostyles lanceolate with a blunt tip; the H:W ranges from 1.46–4.2; height of style rarely more than 0.45 mm. Gastrostyle spines up to 70 μ m long and 15 μ m in diameter, terminating in a clavate tip of crystalline tufts, each about 2.8–3.0 μ m in diameter. Dactylopore spines raised only slightly (0.1–0.2 mm) above the coenosteum; however, their grooves (“dactylotomes”) extend to the bottom of the gastropore valley, or about 0.7–0.8 mm in total length. Width of groove about 0.15 mm; width of dactylopore spine wall between grooves as much as 0.50 mm when the walls are individualized, as little as 0.15 mm when the wall is common.

Dactylozooids adnate, as in *Errinopora* and *Errina*. Large nematocysts, measuring $19.0-21.0 \times 7.0-8.0$ μ m, are common in coenosteal ectoderm and coenosteal canals; smaller nematocysts, $7.0-7.3 \times 3.0-3.5$ μ m, occur in high density in gastro- and dactylozooid tentacles.

Discussion.—*Gyropora* is a monotypic genus.

New Records.—Off Cape of Good Hope, South Africa, depth unknown (found in J. S. Gardiner's coral collection identified as *Distichopora irregularis* (personal communication, H. Zibrowius, 1981)), BM 1977.8.5.1.

Distribution.—Off Cape of Good Hope. 22 m.

Types.—The lectotype (as chosen as Vervoort and Zibrowius, 1981) is deposited at the RMNH (Coel. 13749) and has been examined by the author. The location of the paralectotype is unknown and may be lost.

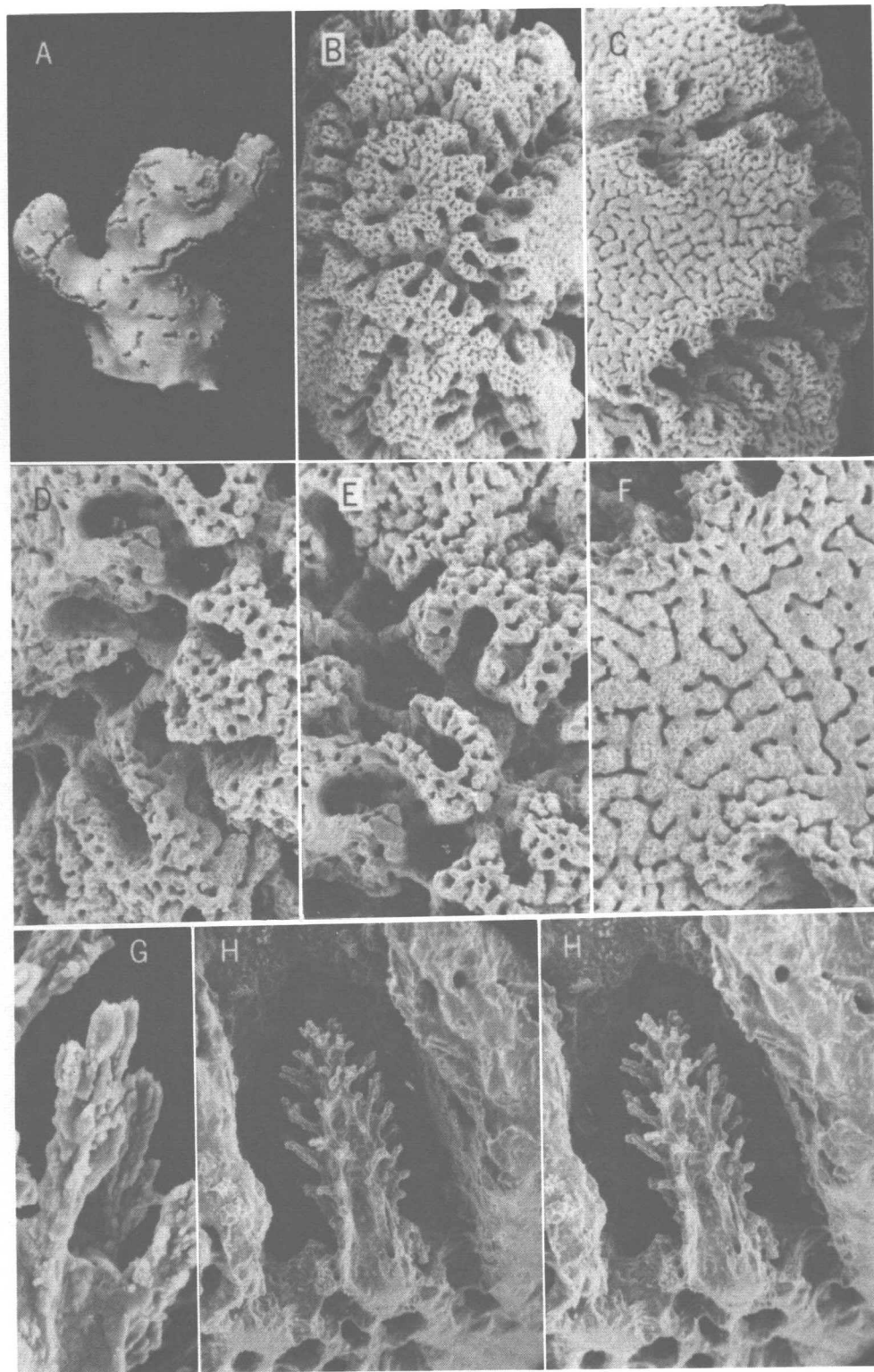
Subfamily Adeloporinae Cairns, 1982

Diagnosis.—Gastro- and dactylopores not arranged in cyclosystems. Gastropores occur at branch tips and axils, each gastropore covered by a hinged operculum.

Adelopora Cairns, 1982

Adelopora Cairns, 1982a: 71.

Figure 13. *Gyropora africana* (A–H, off Cape of Good Hope, BM 1977.8.5.1): A, colony, $\times 1.25$; B–C, top and side of a distal branch, $\times 13$, $\times 15$, respectively; D–E, pore rows, $\times 27$, $\times 33$, respectively; F, reticulate coenosteal texture, $\times 33$; G, gastrostyle spines, $\times 520$; H, gastrostyle, $\times 83$, stereo pair.



Diagnosis.—Colonies flabellate or bushy; branches round in cross section, occasionally anastomosing, especially in flabellate colonies. Coenosteum linear-imbricate, composed of broad, flat platelets; no granules. Gastropores occur at branch tips, branching axils, and, in thicker branches, on lateral surfaces. Gastropore tube cigar shaped, with no style or tabulae; pore covered by a hinged operculum, which, when closed, is flush with the coenosteal surface. Dactylopores are randomly arranged, apically perforate mounds; no dactylostyles. Ampullae large and superficial, some with a lateral, tubular efferent canal.

Discussion.—The complete lack of coordination between the gastro- and dactylopores of *Adelopora*, and its long dactylopore tubes clustered along branch axes, suggests an affinity with the more simple genera of the Errininae. It is most similar to *Pliobothrus*, both genera having apically perforate dactylopore spines, linear-imbricate coenosteal texture, and no gastrostyles. However, *Adelopora* differs significantly in having much better developed and organized coenosteal platelets, smaller coenosteal pores, better-formed gastropore tubes without tabulae, superficial ampullae with large efferent ducts, and gastropores located primarily at branch axils, each covered by a hinged operculum.

Occurrence.—Subantarctic seamounts from off South America and South Pacific. 298–915 m.

Type Species.—*A. pseudothyron* Cairns, 1982, by original designation.

Adelopora pseudothyron Cairns, 1982
Figures 14A–H, 24A–B, 27H–I, 28G

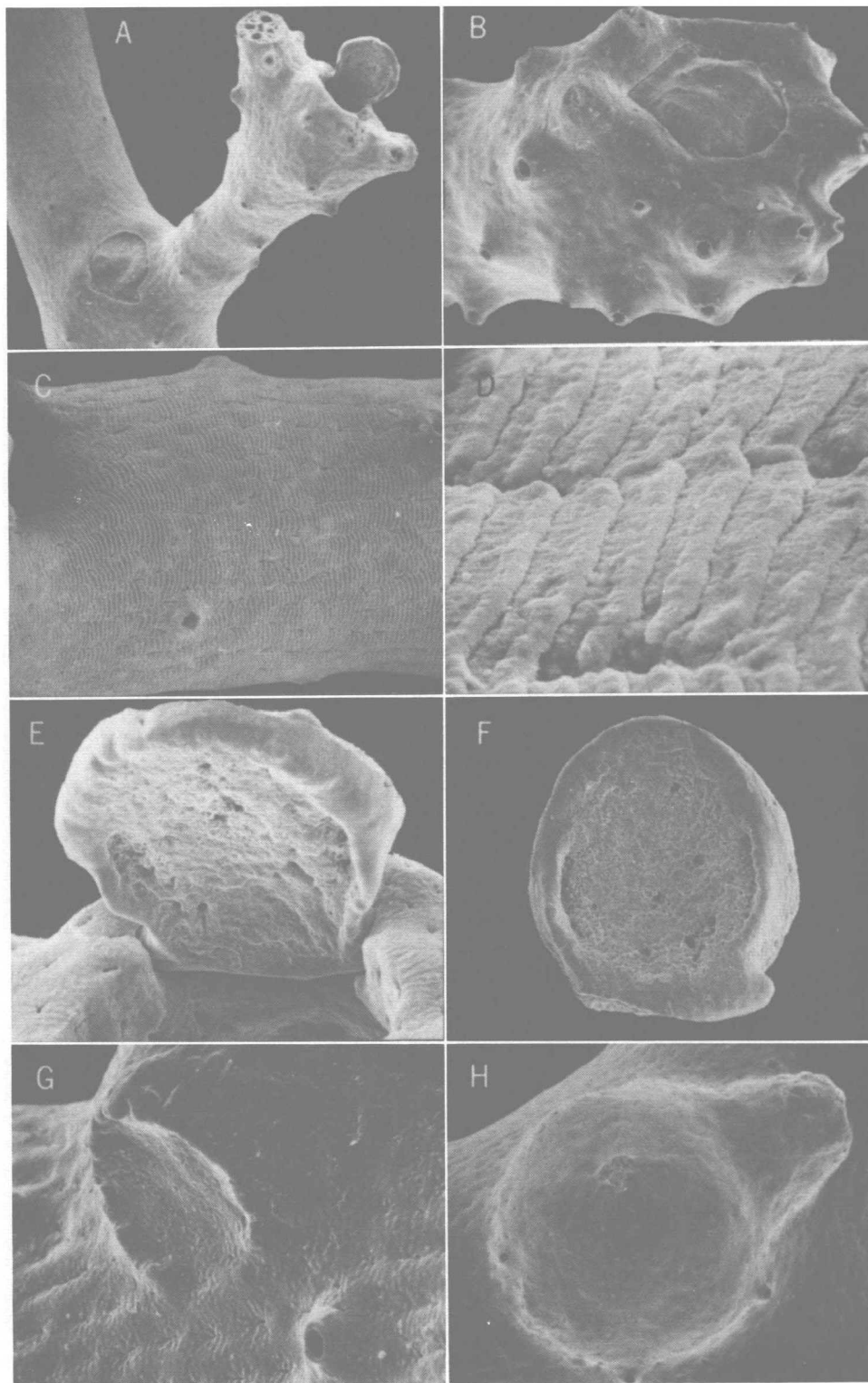
Adelopora pseudothyron Cairns, 1982a: 71–81, figs. 1–22; in press: figs. 31B, 35A–I.

Diagnosis.—Colonies up to 3.8 cm tall; distal branches about 0.9 mm in diameter, basal branches up to 1 cm in diameter. Branching axils often U-shaped. Coenosteal strips 53–70 μm wide, composed of broad platelets extending the entire width of one or two strips; 75–90 leading platelet edges occur per mm. Gastropore tubes at least 1 mm deep and 0.3 mm in diameter, ending in a gently rounded cul-de-sac. Opercula 0.39–0.58 mm long and 0.35–0.64 mm wide with length to width ratios of 0.71–1.34, but averaging about 1.1. Opercula 70 μm thick at their edges but considerably thinner toward the center because of the concavity of their lower sides. Dactylopores 25–35 μm in diameter, occurring only on small diameter distal branches. Dactylopores elevated on mounds up to 0.15 mm tall and 0.15 mm broad at their bases; the pores extend down the center of the branch axis in fascicles for a considerable distance. Ampullae 1.06–1.22 mm in diameter, the efferent canal up to 0.5 mm long and 0.23 mm in distal diameter.

Gastrozooids large, bottle shaped, with a crown of 7–9 relatively long tentacles below a tapered hypostome. Dactylozooids simple and long. Rod-shaped nematocysts measuring 11.8–12.5 \times 2.5–3.0 μm occur in the ectoderm, and oval nematocysts, 6.1–7.0 \times 3.0–3.5 μm , occur on gastrozoid tentacles. Two short

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Figure 14. *Adelopora pseudothyron* (A, paratype from Eltanin 25–326: 46°04'S, 83°55'W, 298 m, 9 Oct. 1966; B–H, paratype from Eltanin-254: 59°49'S, 68°52'W, 512–622 m, 10 Oct. 1962): A, colony with one open and one closed operculum, $\times 23$; B, branch tip with closed operculum and numerous dactylopores, $\times 44$; C–D, imbricate coenosteal texture, $\times 67$, $\times 667$, respectively; E, operculum in open position, $\times 117$; F, underside of operculum removed from corallum, left nub broken off, $\times 95$; G, face of efferent tubule of figure H, $\times 100$; H, ampulla with efferent tubule, $\times 40$.



opercular retractor muscles attach to narrow slits, one on each side of the operculum adjacent to the lower, outer edge (Fig. 28G).

Discussion.—*A. pseudothyron* has been more thoroughly described and illustrated by Cairns (1982a); however, three corrections are made here: (1) the larger coenosteal canals 50–90 μm in diameter described by Cairns (1982a: fig. 22) are actually dactylopore tubes, (2) the gastropore tube is not 1 mm in diameter, but 1 mm long and about 0.3 mm in diameter, and (3) slightly different nematocyst measurements are given in the diagnosis.

Adelopora is a monotypic genus.

Distribution.—Subantarctic seamounts from Scotia Ridge, Drake Passage, Chile Rise, and Eltanin Fracture Zone (South Pacific). 298–915 m.

Types.—Holotype and most paratypes deposited at the USNM. Single paratypes also at BM, ROM, and RMNH.

Subfamily Distichoporinae Stechow, 1921

Diagnosis.—Gastropores linearly arranged, usually on the lateral branch edges, flanked on either side by a row of dactylopores.

Distichopora Lamarck, 1816

Millepora: Pallas, 1766: 288 (part).

Distichopora Lamarck, 1816: 198. — Moseley, 1881: 95. — Broch, 1942: 7–8. — Boschma, 1956: F100; 1959: 121–134.

Madrepora: Nardo, 1844: 68 (part).

Diagnosis.—Colonies usually flabellate, sometimes slightly bushy; branches closely spaced but rarely anastomotic. Branches usually elliptical to rectangular in cross section, the greater branch axis in the plane of the colony; branch tips usually blunt. Coenosteal texture tuberculate to reticulate, always covered by low granules; low, longitudinal supporting ridges sometimes present. Color of coenosteum highly variable. Gastro- and dactylopores extend for a long distance down the center of the branch. Gastropores aligned or slightly staggered in pore rows, which run along the lateral branch edges, sometimes meandering over the branch faces. Gastropores usually flanked on both sides by a row of dactylopores; however, sometimes only one side has pores or one side has a greater frequency and/or height of dactylopores. Gastropores round to polygonal, sometimes sunken along a recessed sulcus or flush with the coenosteum. Dactylopores oval to elliptical, their greater axis perpendicular to the pore row; dactylopores may be elevated (in which case a short dactylotome is present), conical, or flush with the surface. No dactylostyles. Gastrostyles needle shaped (H:W often over 10) and very prominently ridged, the ridges bearing tall, pointed spines. A diffuse ring palisade is often present and tabulae sometimes stabilize the style. Female ampullae superficial and often ridged in a stellate or longitudinal fashion; male ampullae smaller. Ampullae are often clustered.

Discussion.—*Distichopora* is most similar to the genus *Sporadopora*. Both have very long gastro- and dactylopores, and sacs which completely enclose the gastrozooids, characters shared only by the simple Errininae. Furthermore, both have extremely long, ridged gastrostyles supported by tabulae (a character shared only by these two genera), reticulate coenosteum on the older branches, flush gastro- and dactylopores (some *Distichopora*), blunt branch tips, and no dactylostyles. *Distichopora* differs primarily in its linear coordination of gastro- and dactylo-

pores, elliptical dactylopores, and superficial ampullae. One species, *D. providentiae* (Hickson and England, 1909), seems to be transitional between the two genera. It has distichoporine-shaped dactylopores and partially buried ampullae, but the coordination of its dactylo- and gastropores is not as intimate as in the other *Distichopora*, and in some places it is almost random (Fig. 16H). Both Hickson and England (1909) and Boschma (1959) considered *D. providentiae* to represent an intermediate between the two genera, the former placing it in *Sporadopora*, the latter transferring it to *Distichopora*. I agree with Boschma, that *D. providentiae* is more similar to the other species of *Distichopora* and that it may resemble a transitional stage between *Sporadopora* and *Distichopora*.

Occurrence.—Eocene: Paris; Miocene: New Zealand; Pliocene: Japan; Recent: Indo-West Pacific, North Pacific, off Galapagos (undescribed species from Albatross station 2818: 0°29'S, 89°54'30"W, 717 m, USNM), western Atlantic. 1–717 m.

Type Species.—*Millepora violacea* Pallas, 1766, by monotypy.

Distichopora (Distichopora) violacea (Pallas, 1766)
Figures 15A–H, 26C, 27D

Millepora violacea Pallas, 1766: 258.

Distichopora violacea: Lamarck, 1816: 198.—Hickson, 1892: 501–507, pl. 18, figs. 1–4, pl. 19, figs. 1–3; 1893: 129–153, pl. 9, figs. 1–18.—Hickson and England, 1909: 346–348.—England, 1926: 275–278, text-figs. 12–18.—Boschma, 1956: F100, fig. 83, 2a; 1957: 47–48; 1959: 134–144, pl. 1, figs. 2–17, pl. 2, figs. 3–8, pl. 3, figs. 1–3, pl. 4, figs. 1–3, 6–13, pl. 5, figs. 1–4, pl. 6, figs. 1–2, 4, pl. 14, figs. 3–4 (detailed synonymy and discussion).—Eguchi, 1965: 219; 1968: 38–40, pl. 25, figs. 3–5, pl. 26, figs. 3–5, 18, pl. 27, figs. 4–5.—Boschma, 1968d: 13–14, fig. 5.—Fenninger and Flajs, 1974: 71, 75, pl. 5, fig. 6.—Chevalier, 1978: 245, 273; 1979: 132.—?Rønneberg, Fox and Liaaen-Jensen, 1979: 408.

Distichopora cinabarina Nardo, 1844: 62.—Boschma, 1959: 139.

Madrepora violacea: Nardo, 1844: 68.

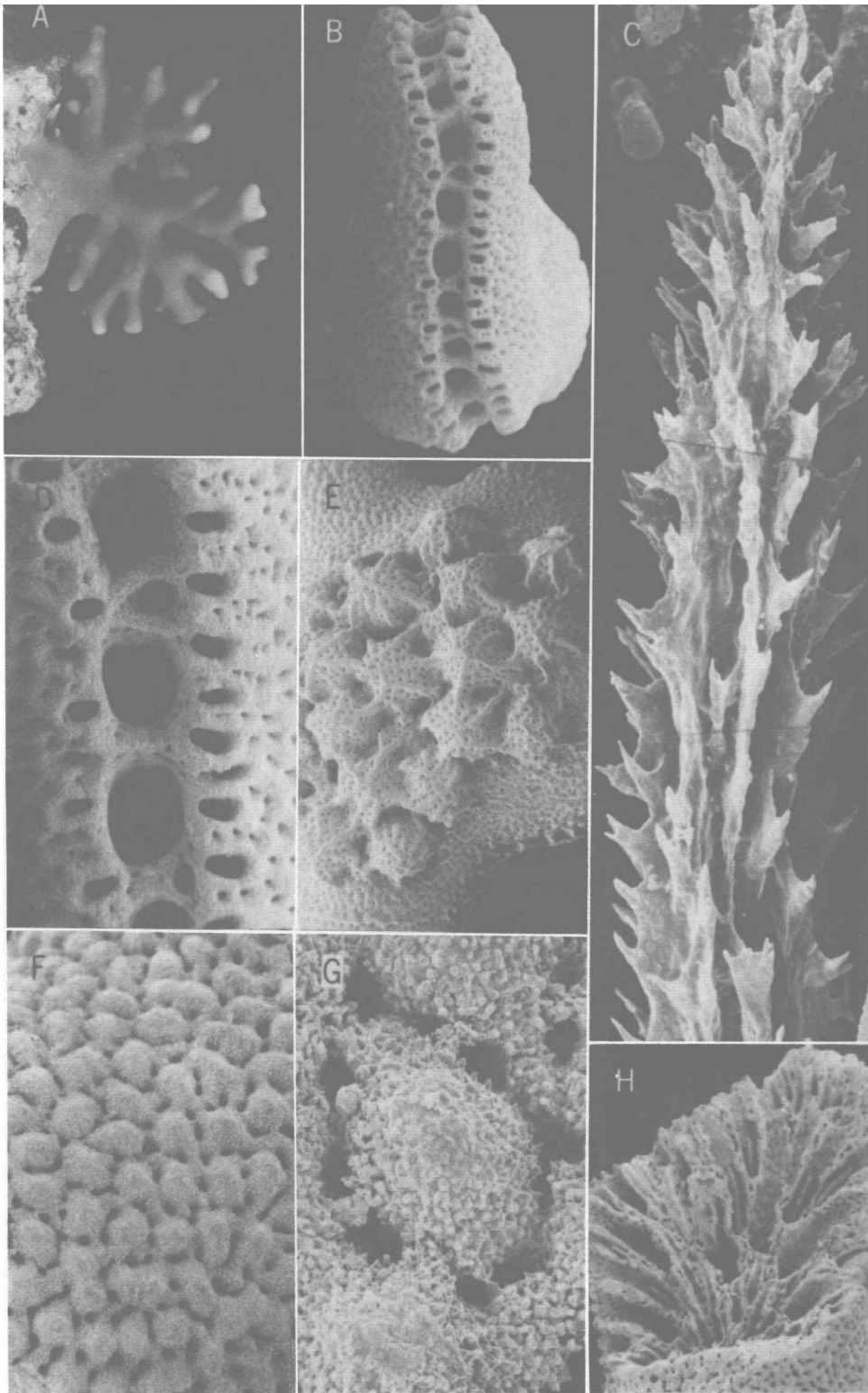
?*Distichopora fulvacea* Michelin, 1862: Annexe B.—Boschma, 1959: 152–153.

?*Distichopora rosea* Kent, 1871: 281.—Boschma, 1959: 139.

Distichopora fisheri Broch, 1942: 14–16, pl. 2, fig. 3, text-fig. 2, 30a.—Wells, 1954: 476, pl. 185, figs. 1–2.

Not *Distichopora violacea*: Broch, 1942: 9–14, pl. 1, figs. 1–2 (= *D. nitida* and *D. coccinea*).—Wells, 1954: 476, pl. 185, fig. 3 (= *D. nitida*).

Diagnosis.—Colonies flabellate, rarely exceeding 8–9 cm in height. Branches compressed in plane of fan, blunt tipped, and closely spaced. Colony form variable: forma *violacea* s.s. broadly flabellate with thick terminal branches (2.5 × 3.0–5.0 mm in diameter); forma *fisheri* flabellate but vertical branch growth predominates, terminal branches as in *violacea* s.s.; forma *tenella* broadly flabellate but terminal branches slender (1.5 × 2.5 mm in diameter). Intergrades and other variations of colony form and branch thickness also occur. Base of colony usually forms a broad encrustation. Coenosteum at branch tips tuberculate, composed of discrete convex tubercles measuring 0.15–0.20 mm in diameter, each surrounded by 5–8 round coenosteal pores 35–39 µm in diameter; tubercles covered by rounded granules 8–10 µm in diameter. Towards the colony base the tubercles fuse, creating a reticulate texture. Coenosteum usually violet or red but may be vermilion, pink, orange, brown, yellow, or white. Pore rows generally restricted to lateral branch edges but occasionally meandering over anterior or posterior faces; short rows running perpendicular to the lateral rows are common at branch tips; isolated rows of 1–4 gastropores also occur on the branch faces near the base of the colony, often resembling cyclosystems. Pore rows 0.8–1.0 mm in width, sulcus depth varies from shallow to deep. Gastropores round to polygonal, 0.3–0.5 mm in



diameter, usually arranged unilinearly. Dactylopores about 0.19 mm long and 0.06–0.08 mm wide, the pores narrowing to a lesser width near the gastropore. Dactylopores only slightly raised; dactylotomes correspondingly short. Approximately 2.1–2.9 gastropores per mm and 4.0–4.5 dactylopores per mm, the dactylopores of equal frequency on either side of the pore row, thus 3–4 dactylopores per gastropore. Illustrated gastrostyle 0.55 mm tall, 0.064 mm wide (H:W = 8.5), bearing tall (up to 35 μ m) sharp, upcurved, claw-like spines on its ridges. Diffuse ring palisade composed of clavate elements measuring up to 54 μ m tall and 16–18 μ m in diameter; no tabulae noted. Female ampullae 0.6–1.0 mm in diameter, usually bearing radiating ridges; male ampullae smaller and usually clustered into a large mass.

Gastrozooids with 4–6 tentacles; dactylozooids adnate. Ectodermal nematocysts oval, 6.5–8.0 \times 3.2–4.0 μ m; those of gastrozooid tentacles and dactylozooids rod shaped, 4.0 \times 1.5–2.0 μ m. Sexes usually separate but hermaphrodites do occur. Male ampullae may have 4–5 gonophores apiece.

Discussion.—The history of the synonymy of *D. violacea* and a comparison to other species is given by Boschma (1959); remarks on its gonophores are made by Hickson (1893) and England (1926); and a description of the histology of the polyps and coenosteum is given by Hickson (1892).

Fifteen Recent species are assigned to *Distichopora* (Table 1): nine in the Indo-West Pacific region, one in the North Pacific, and five in the western Atlantic. In addition, three fossil species are known from the Eocene of Paris, Miocene of New Zealand, and Pliocene of Japan. I have examined representatives of all but three (*D. livida*, *D. sepens*, *D. profunda*) of the Recent species.

Distribution.—From the western Indian Ocean to the central Pacific, but not Hawaii (see Boschma, 1959: 144). Shallow water to 122 m.

Types.—Deposition unknown.

Subgenus *Distichopora* (*Haplomerismos*) Cairns, 1978

Distichopora (*Haplomerismos*) Cairns, 1978: 84.

Diagnosis.—Colonies small and flabellate, the flabellum sometimes slightly curved. After initial bifurcation of main stem no further branching occurs; instead, two vertically flattened lobes are produced which grow in opposite directions and parallel to the substrate. Coenosteum flat and granular (not reticulate), bearing low longitudinal ridges. Gastro- and dactylopores are both very long, extending for a great distance down the center of the lobes. Pore rows occur on lateral edges of lobes and main stem. Dactylopores occur in about equal number on both sides of pore rows. Gastrostyles have a very high H:W and are ridged, the ridges bearing tall, slender, often fused, spines; no ring palisade. Ampullae internal, opening to surface by irregularly shaped pores.

Discussion.—*Haplomerismos* differs from the nominate subgenus primarily in its unusual colony shape and its nonreticulate coenosteal texture. Other points of

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Figure 15. *Distichopora violacea* (A, Johnson Atoll; B–D, F–H, Pa'ea, Tahiti, USNM 43284; E, Gekei Atoll, Marshall Islands): A, colony, $\times 1.6$; B, D, pore row, $\times 16$, $\times 40$, respectively; C, gastrostyle tip, $\times 350$; E, clustered ampullae, $\times 15$; F–G, tuberculate coenosteal texture, $\times 37$, $\times 165$, respectively; H, longitudinal branch fracture revealing gastrostyles, $\times 15$.

difference include its gastrostyle spines, which are more slender and often fused, and its internal ampullae, both characters shared with the aberrant *D. providentiae*. The bilobate colonial form is unique among the Stylasterina. Several species of *Distichopora*, particularly *D. borealis*, have broad, flattened branch tips approximating a small lobe, but eventually bifurcation occurs producing an arborescent colony. Only one other species is known to have plate-like fronds: some specimens of *Errinopora nanneca* have large, vertical, solid flabella. *Stylanthea porphyra* also has a broad, flat coenosteal surface, but it is an encrusting species.

Occurrence.—Known only from off Laysan, Hawaiian Islands. 658–736 m.

Type Species.—*D. (Haplomerismos) anceps* Cairns, 1978, by original designation.

Distichopora (Haplomerismos) anceps Cairns, 1978
Figures 16A–G, 24C, 25F, 28E

Distichopora (Haplomerismos) anceps Cairns, 1978: 84–86, pl. 1, figs. 1–6.

Diagnosis.—Colonies up to 26.4 mm tall and 49.2 mm broad; main stem 4–5 mm in diameter and about 12 mm tall. Lobes 2.5–3.5 mm thick and usually slightly asymmetrical, one being larger than the other. Coenosteal granules rounded to conical, 15–30 μ m in diameter and equally tall; coenosteal pores irregular in outline, 20–30 μ m in diameter. Both granules and pores randomly scattered over the coenosteum, the pores much less numerous. Coenosteum white. Pore row about 1 mm wide, containing a recessed sulcus about 0.6 mm deep. Gastropores elliptical to rectangular, up to 0.75 mm long and 0.36 mm wide, the greater axis aligned with the sulcus. Gastropores regularly and unilinearly arranged, separated by thin septa; up to 15 pores per cm. Dactylopores elliptical in cross section, up to 0.35 mm long and 0.18 mm wide, oriented with their greater axes perpendicular to the pore row; no dactylotome; up to 30 pores per cm. Sometimes the dactylopores on one side of the pore row are taller and fewer in number. Gastrostyles sometimes exceed 5.5 mm in length with an average diameter of 0.085 mm, producing H:W ratios in excess of 65. Styles bear elongate, slender spines up to 75 μ m long and 6 μ m in diameter, which project perpendicularly or slightly toward the tip of the style. Internal diameter of female ampullae 1.0–1.14 mm.

Gastrozooids short and squat in the contracted state, concentrated near the tip of the gastrostyle; gastrozooids orange in alcohol. Adnate dactylozooids long and slender, attached to an adhesive basal structure which is robust below the junction but long and ribbonlike above. Nematocysts of gastrozooid tentacles and dactylozooid tips small, measuring 5.0–6.0 \times 2.3–2.5 μ m; those of coenosteal canals only slightly larger: 7.3–8.0 \times 2.7–3.0 μ m. Gonophores not examined.

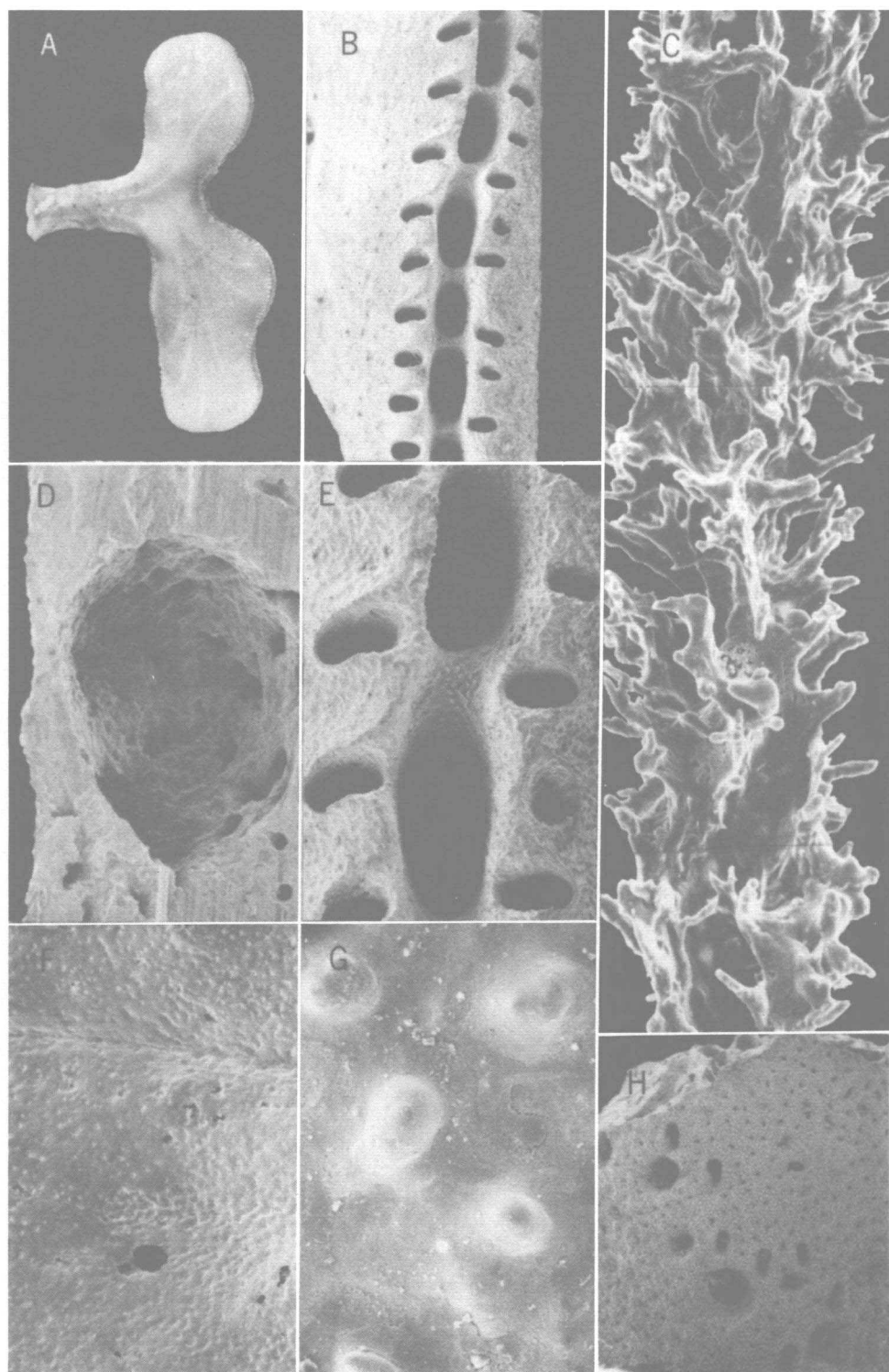
Discussion.—*Haplomerismos* is monotypic; the type-species has been more thoroughly described by Cairns (1978).

Distribution.—As for the genus.

Types.—The holotype and three paratypes are deposited at the USNM.

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Figure 16. *D. (Haplomerismos) anceps* (A–G, paratypes from off Laysan): A, colony, $\times 1.4$; B, E, pore row, $\times 15$, $\times 34$, respectively; C, midsection of a gastrostyle, $\times 270$; D, cross section of an internal ampulla, $\times 40$; F, coenosteal surface with ridge, $\times 30$; G, coenosteal granules, $\times 500$. *Distichopora providentiae*: H, syntype from Percy Sladen Trust Expd. station D-8: off Providence Island, 229 m, BM 1957.2.18.2, branch segment with irregular pore row, $\times 20$.



Subfamily Stylasterinae Gray, 1847

Diagnosis.—Gastro- and dactylopores arranged in distinct cyclosystems.

Stylaster Gray, 1831
Group A ("*Allopora*")

- Allopora* Ehrenberg, 1834: 303, 371.—Milne Edwards and Haime, 1857: 131.—Moseley, 1881: 91, 96–97.—Fisher, 1938: 503.—Boschma, 1956: F99–100.
Stylaster: Milne Edwards and Haime, 1857: 131 (part: third section).—Studer, 1878: 635 (part: third group).—Hickson and England, 1905: 7 (part: group C).
Dendracis: Römer, 1863: 243 (part).
Cryptaxis Reuss, 1865: 620.
Stylaster (Allopora): Broch, 1914: 7; 1936: 9.
Cryptaxiella Kühn, 1939: A-31.

Diagnosis.—Colonies flabellate to bushy, often massive. Branches cylindrical to slightly compressed and blunt; branch anastomosis occurs in some species. Coenosteum reticulate, covered by rounded or irregularly shaped granules; coenosteum white, orange, red, pink, purple, yellow, or blue. Coenosteal papillae (small mounds) and short, flattened coenosteal outgrowths present in some species. Cyclosystems uniformly spaced on all sides of branches. Gastrostyles quite variable in shape, ranging from almost hemispherical ($H:W = 1$), to bullet shaped ($H:W = 2-5$), to lanceolate ($H:W$ up to 10). Gastrostyles longitudinally ridged and usually highly spinose; ring palisade often present; tabulae rarely present. Three to seventeen dactylopores per cyclosystem; however, 7–9 are the most common numbers; diastemas rare. Additional isolated dactylopores often present, sometimes in great numbers. Dactylostyles well developed, composed of long cylindrical elements, but not present in isolated dactylopores. Ampullae low superficial bulges, sometimes ridged.

Group B (Annectant group)

- Stylaster* Gray, 1831: 37 (part).—Milne Edwards and Haime, 1857: 130 (part: second section).—Studer, 1878: 634 (part: second group).—Hickson and England, 1905: 7 (part: group B).
Stylaster (Eustylaster): Broch, 1914: 7 (part: group B).
Stylaster (Eu-Stylaster): Broch, 1936: 9 (part).

Diagnosis.—Like Group C, but in addition to the regularly sympodially arranged cyclosystems at the branch tips there are additional cyclosystems on the anterior and posterior branch faces, especially on the larger diameter branches. Colonies usually slightly more robust, sometimes bushy.

Group C ("*Stylaster*")

- Stylaster* Gray, 1831: 37 (part).—Milne Edwards and Haime, 1857: 128 (part: first section).—Studer, 1878: 634 (part: first group).—Moseley, 1881: 91, 97.—Hickson and England, 1905: 7 (part: group A).—Fisher, 1938: 498–499.—Boschma, 1956: F99.
Cyclopora Verrill, 1866: 38.
Deontopora Hall, 1893: 117.
Stylaster (Eustylaster): Broch, 1914: 7 (part: group A).
Stylaster (Eu-Stylaster): Broch, 1936: 9 (part).

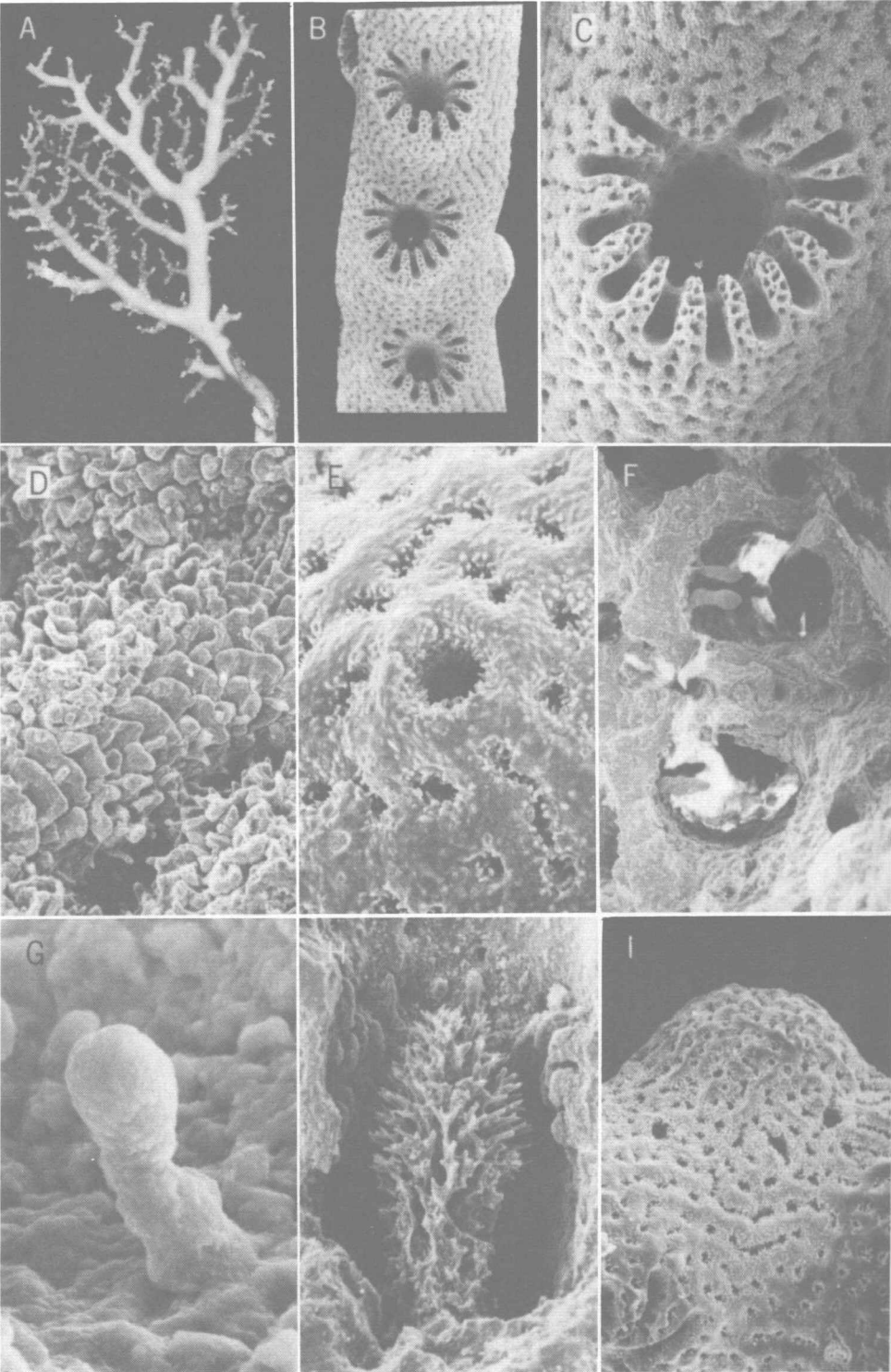
Diagnosis.—Colonies flabellate and delicate. Branches usually slender, terminating in a characteristic zigzag, sympodial shape. Branches elliptical in cross section and sometimes anastomose, even approaching the fenestrate growth form of *Erinopsis*. Coenosteum variable in texture, including reticulate-granular, linear-imbricate, and very irregular reticulate-imbricate. Papillae (nematopores ?) and

short ridges are sometimes present on the coenosteum. Coenosteum orange, beige, purple, or white. Cyclosystems occur in a regularly sympodial pattern resulting in two rows, one on each lateral branch edge. These rows may be displaced to the anterolateral edges of large diameter branches but cyclosystems do not occur on the anterior or posterior branch faces. Cyclosystems usually slightly raised above the coenosteum, especially the abcauline side, which gives them an anteriorly projecting aspect. Gastrostyles lanceolate and ridged, with a medium to high H:W ratio, and invariably with a well-developed ring palisade. Usually 10–15 dactylopores per cyclosystem; adcauline diastemas not uncommon; dactylostyles rudimentary. Ampullae large and superficial, sometimes ridged.

Discussion.—The problem of distinguishing *Stylaster* from *Allopora* has been discussed by many authors and has undoubtedly been the cause of great frustration. Typical representatives of the two genera are clearly quite different but species with intermediate characters are common. Milne Edwards and Haime (1857: 131) were the first to suggest dividing *Stylaster* into three groups: the first corresponding to my Group C, their second to my annectant Group B, and their third to my Group A. They also maintained the genus *Allopora*, distinguishing it by a more irregular branching and a smoother coenosteum. Studer (1878) accepted this scheme as did Hickson and England (1905: 6–7), who introduced a fourth group (D), which we now know as *Stenohelia*. Moseley (1881: 90–91, 97) acknowledged the problem but maintained two separate genera: *Stylaster* (my Groups B and C) and *Allopora* (my Group A). He differentiated them on the regularity of arrangement of cyclosystems and number of tentacles per gastrozoid. Broch (1914: 7; 1936: 8–11) admitted that there was no definite hiatus between *Allopora* and *Stylaster* but nonetheless established subgenera to name his groups: *S. (Eustylaster)*, my Groups C and B; *S. (Allopora)*, my Group A; and *S. (Stenohelia)*, *Stenohelia*. Fisher (1938: 498–499) pointed out that establishing subgenera does not solve the inherent problem of where to place an annectant species. His faunistic account employed only *Stylaster* (my Group C) and *Allopora* (my Groups A and B). Boschma (1956: F99–100) presented the two genera as distinct with no further explanation, and in 1965c he discussed the problem and gave a short history of the debate. All recent papers have used *Allopora* and *Stylaster* as distinct genera.

I have examined representatives of about two-thirds of the valid taxa that I have listed for this species complex and, like those before me, can find no discontinuity between the two genera. Intermediates exist which have cyclosystem arrangements typical of both genera on the same colony. I have therefore synonymized *Allopora* with *Stylaster* but, because this produces a large genus containing about one-third of the stylasterine species, I have divided the genus into three groups, a variation of the solution of Milne Edwards and Haime (1857). The groups have no taxonomic standing and are created for convenience only.

To reiterate, my Group A (“*Allopora*” of others) is characterized by having bushy to flabellate, robust colonies; thick cylindrical branches; reticulate-granular coenosteum; low or flush cyclosystems on all sides of the branches; well-developed dactylostyles; and low, superficial ampullae. Group C (“*Stylaster*” of others) is characterized by having delicate flabellate colonies; thin, flattened branches; variable coenosteal texture (including imbricate); raised cyclosystems arranged in two rows on the lateral branch edges; rudimentary dactylostyles; and large, superficial ampullae. The annectant Group B has characters intermediate between the two. The most significant character separating Groups A and C is the arrangement of the cyclosystems. No other character consistently distinguished the two; however, if more species are examined histologically and by scanning electron microscopy, a more valid division may be proposed in the future.



Stylaster (Group A) is very similar to *Errinopora*, as previously stated. Both Group A and certain species of *Errinopora* (i.e., *E. pourtalesii*, *E. styliifera*) have similar colony and branch shapes, coenosteal texture (including papillae), gastro- and dactylostyles, isolated dactylopores flush with the coenosteum, and superficial ampullae. The main difference between the two is the greater coordination of gastro- and dactylopores as distinct cyclosystems in Group A; however, as previously noted, isolated gastropores on basal branches of *Errinopora* are sometimes surrounded by dactylopores, resulting in rudimentary cyclosystems (pseudocyclosystems). Although cyclosystems are characteristic of all *Stylaster* and rudimentary ones are found in some *Errinopora*, it is not difficult to hypothesize that the ancestor of Group A evolved from an *Errinopora*-type stock by a selection for the pseudocyclosystem arrangement of pores and a consistent lateral fusion of dactylopore spines, as has occurred in *E. cestoporina* and *Gyropora*, resulting in true, highly coordinated cyclosystems.

Occurrence.—Group A is known from the Oligocene of Germany and Washington; the Atlantic, Pacific, and Antarctic Oceans; and off South Africa (not Indian Ocean). Group B is known from the Miocene of Czechoslovakia and from the Atlantic, Pacific, and Antarctic Oceans (not Indian Ocean). Group C is known from the ?Oligocene of Italy, Eocene of Madagascar and Tonga, Miocene of Australia and Japan, and from all ocean basins. (Undescribed species in the USNM collections are from Hawaii and the Galapagos.) 1–1,400 m.

Type Species.—*Madrepora rosea* Pallas, 1766, by subsequent designation (Milne Edwards and Haime, 1850); a member of Group B.

Stylaster roseus (Pallas, 1766)
Figures 17A–I, 25A, 26D, 28F, H

Madrepora rosea Pallas, 1766: 312.

Oculina rosea: Lamarck, 1816: 287.

Stylaster roseus: Gray, 1831: 37.—Milne Edwards and Haime, 1857: 130.—Pourtales, 1871: 83.—Boschma, 1955: 134–138; 1956: F99, fig. 80, 1; 1957: 14–15 (synonymy).—Goedbloed, 1962a: 442–445, text-figs. 11–17; 1962b: 529–531, text-figs. 22–26.—Boschma, 1965c: 227–247, pl. 1–3, text-figs. 1–4 (explicated synonymy).—Fox, 1972: 921–922.—Kruijff, 1977: 445–450, text-figs. 1–3, 5.—Cairns, 1982b: 274, fig. 119d–e.

Millepora rosacea: Nardo, 1845: 637.

Allopora rosea: Dana, 1848: 694.

Not *Stylaster roseus*: Perrier, 1881: 303.—Filhol, 1885: 268.—Krämer, 1897: 104.—Broch, 1914: 12–15 (= *S. erubescens*).—Boone, 1933: 31.

Not *Stylaster* (*Eu-Stylaster*) *roseus*: Broch, 1936: 15 (= *S. erubescens*).

Stylaster (*Eustylaster*) *duchassaingii*: Laborel, 1971: 224, pl. 8, fig. 4.

Diagnosis.—Colonies flabellate to bushy, up to 7 cm tall and 11 cm broad. Branches slightly elliptical in cross section and nonanastomotic; distal branches not much larger in diameter than diameter of a cyclosystem (about 1 mm). Coenosteum linear-imbricate with a tendency toward reticulate structure near ampullae and cyclosystems. Strips usually 65–80 μ m wide, covered by a very irregular arrangement of platelets measuring 5–34 μ m in width. Slits separating strips narrow and

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Figure 17. *Stylaster roseus* (A–I, Carrie Bow Cay, Belize, 8–10 m, USNM 47807): A, colony, $\times 0.9$; B, cyclosystem on lateral branch edge, $\times 19$; C, individual cyclosystem, $\times 50$; D, imbricate coenosteal texture, $\times 380$; E, isolated dactylopore, $\times 200$; F, two dactylopores with dactylostyles, $\times 270$; G, dactylostyle element, $\times 1,470$; H, gastrostyle and ring palisade, $\times 133$; I, ampulla, $\times 53$.

deep, bearing elongate granules. Coenosteum rose, red, light purple, or yellowish. Cyclosystems variable in their arrangements. Usually on distal branches they are arranged in a regularly sympodial manner which may continue throughout the colony or be augmented by additional cyclosystems on the anterior and posterior sides. Some colonies have entirely regularly sympodially arranged cyclosystems; on others they are mostly randomly arranged; and yet others have both arrangements on different branches of the same colony. It appears that bushy colonies have a greater tendency for the irregular arrangement. Cyclosystems round to slightly elliptical, 0.75–1.0 mm in diameter. Gastrostyles lanceolate and highly ridged, measuring 0.32–0.50 mm tall and 0.11–0.20 mm in diameter (H:W = 2.1–3.6). Gastrostyle spines fused along ridges; they are slender and pointed, up to 32 μ m long. A distinct ring palisade is present, encircling the upper third of the style, composed of vertical ridges up to 52 μ m long and 15 μ m wide. Based on 1,003 cyclosystems, Boschma (1965c) found the range of dactylopores per cyclosystem to be 5–15, average = 9.7, and mode = 10. Both dactylotomes and pseudosepta are about 60–70 μ m wide; however, a small adcauline diastema is sometimes present, measuring 3–4 times the width of a pseudoseptum. Dactylostyles rudimentary, composed of widely spaced, linearly arranged, cylindrical to clavate elements 25–27 μ m tall and 11 μ m in greatest diameter. Ampullae very prominent, 0.5–0.7 mm in diameter, with a thin, porous surface which may be smooth or warty. Sometimes there is a small porous indentation about 0.17 mm in diameter near the base of the ampulla: the future efferent duct. Ampullae are often clustered on both the anterior and posterior sides.

Gastrozooids are short, blunt cylinders, each with several tentacles. Dactylozoid tentacles within cyclosystems are usually adnate (Goedbloed, 1962a); however, some are simple and greatly elongated (hair dactylozooids of Kruijf, 1977). Isolated simple dactylozooids also occur with varying frequency. Nematocysts of gastrozoid tentacles and dactylozooids about $6 \times 2 \mu$ m; slightly larger swollen nematocysts measuring $7 \times 4 \mu$ m occur on the pseudosepta. Colonies may be hermaphroditic, but individual ampullae are exclusively male or female (Goedbloed, 1962b).

Discussion.—As I have divided the genus *Stylaster* (Table 1), Group A contains 24 species, 1 subspecies, and 1 forma; Group B has 16 species and 4 subspecies; Group C has 26 species, 5 formae, and 2 unnamed species; two more species are *nomina nuda*. *Stylaster* s.l. thus contains 68 species (plus 2 *nomina nuda*), 5 subspecies, and 6 formae, or a total of 79 taxa. *S. roseus* belongs in the annectant Group B, “a rather unfortunate choice” of the type-species, according to Boschma (1965c: 232), because of its intermediate position between *Stylaster* and *Allopora*.

Boschma (1955; 1965c) discussed the synonymy and morphology of *S. roseus* in great detail. Goedbloed (1962a; b) examined its dactylozooids and gonophores, and Kruijf (1977) reported on its polyp behavior and sweeping tentacles. Other important works dealing with the soft anatomy or natural history of other species of *Stylaster* s.l. include: Moseley (1881: 57–65), Hickson (1890), Broch (1914: 8–19; 1942: 73–77), England (1926), and Ostarello (1973; 1976).

Distribution.—Caribbean and off Brazil to Pernambuco (not Gulf of Mexico or Florida Keys). Most common between 0.5–4 m.

Types.—Pallas's types have not been traced.

Stylantheca Fisher, 1931

Stylantheca Fisher, 1931: 395.—Boschma, 1956: F100.

Allopora: Fisher, 1938: 528 (part).

Stylaster (Allopora): Broch, 1942: 101 (part).

Stylaster (Stylanthea): Boschma, 1951: 39.

Diagnosis.—Colonies encrusting, forming thin laminae on rocks and shells. Coenosteum reticulate-granular, purple to light pink, and bears numerous small, apically perforate papillae. Cyclosystems round to elliptical, each bearing 1–12 gastrozooids and gastrostyles. Gastrostyles globose to conical, squat (H:W usually less than 2), and vertically ridged; the ridges bearing long, slender spines. A prominent ring palisade originates from the common spongy horizontal gastropore floor, below which the gastrostyles are housed in individual gastrostyle chambers. Three to sixteen dactylopores per cyclosystem; isolated dactylopores uncommon. Inner edge of dactylotome deep, revealing a well-developed dactylostyle. Ampullae internal, often massed together or encircling a cyclosystem, alternating with the dactylopores.

Discussion.—*Stylanthea* is very similar to *Stylaster* (Group A); several authors have synonymized the two or treated *Stylanthea* as a subgenus. It differs from *Stylaster* (Group A) primarily in its encrusting habit and its tendency to have more than one gastrozooid per cyclosystem, both of which are characters unique in the Stylasterina. For these reasons *Stylanthea* is kept as a separate genus. *Stylaster verrillii* (Dall, 1884) also forms lumpy encrustations but also develops into upright lobes and normal arborescent colonies (Fisher, 1938: 521). In the case of *S. verrillii* the encrusting colonies are probably just a stage in the development of larger branched colonies. Two other characters that unite the species of *Stylanthea*, and serve to differentiate them from most *Stylaster*, are their well-developed coenosteal papillae and their very deep dactylotome slits.

Occurrence.—Recent: Northeast Pacific from California to Alaska. 0–18 m.

Type Species.—*Stylanthea porphyra* Fisher, 1931, by monotypy.

Stylanthea porphyra Fisher, 1931

Figures 18A–I, 24H, 27G, J

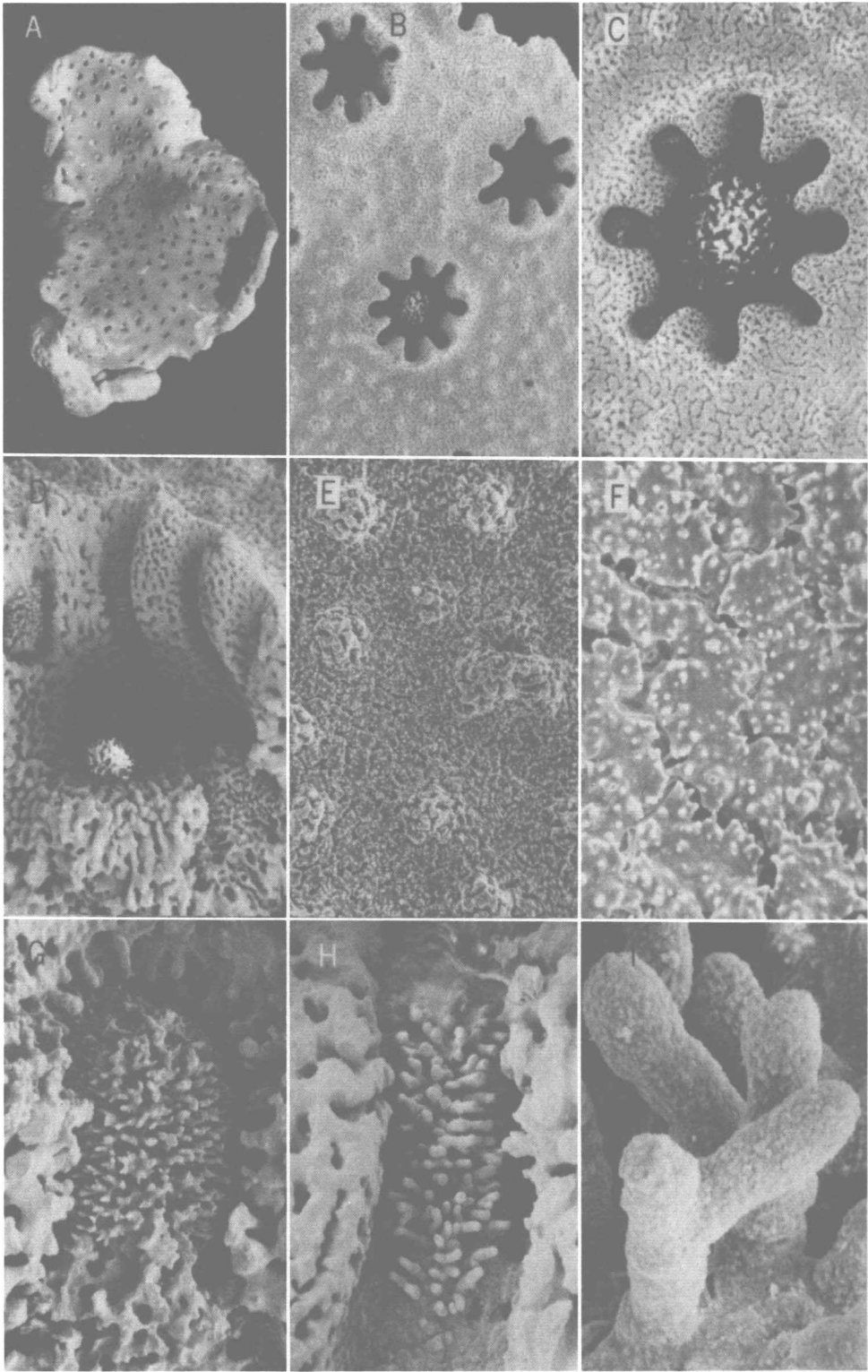
Stylanthea porphyra Fisher, 1931: 395–397, pl. 15, fig. 1, pl. 16, fig. 5, pl. 17, fig. 6.—Boschma, 1956: F100, text-fig. 81, 1; 1957: 33; 1960: 426–427, text-fig. 1e–f; 1961: 221.

Allopora porphyra: Fisher, 1938: 528–530, pl. 59, figs. 1–2, pl. 60, pl. 61, fig. 1, pl. 70, fig. 2.

Stylaster (Allopora) porphyrus: Broch, 1942: 101.

Stylaster (Stylanthea) porphyra: Boschma, 1951: 39, text fig. 5b.

Diagnosis.—Encrustations up to 30 × 25 cm, about 2.5 mm thick. Coenosteal strips flat, 25–55 μ m wide, separated by deep slits about 7.5 μ m wide; granules 3–7 μ m in diameter, pointed. Coenosteal papillae uniformly spaced about 1 diameter from each other, fused into parallel rows, or absent altogether from portions of the colony. Papillae 0.07–0.19 mm in diameter and up to 0.24 mm tall, having an irregularly shaped apical pore measuring about 17 μ m in diameter. Cyclosystems round to elongate; the most elongate appear to be multiple cyclosystems fused together. Round cyclosystems 1.0–1.1 mm in diameter, elongate ones up to 2.7 × 1.0 mm in size. Cyclosystems usually only slightly raised above coenosteum, more rarely elevated up to 2 mm with short coenosteal costae radiating from the dactylotome edges. One to 12 gastrostyles per cyclosystem (Fisher, 1938): in a sample of 31 cyclosystems examined from the type-specimens, a range of 1–8 was found, average = 3.3 (σ = 1.59), mode = 3. Gastrostyles globose and very irregular, 0.40–0.43 mm high, 0.26–0.33 mm broad, with H:W ranging from 1.2–1.6. Gastrostyle spines up to 80 μ m long and 7 μ m in diameter, pointed, and usually fused to adjacent spines near the underlying ridge. In a sample of 34 cyclosystems, the range of dactylopores per cyclosystem was 6–16, average 9.11



($\sigma = 2.08$), mode = 10. Dactylostyles up to 0.35 mm long and 0.09 mm wide, composed of long, blunt, cylindrical elements up to 50 μm long and 10 μm in diameter. Elements of ring palisade similar but shorter. Male ampullae about 0.3 mm in internal diameter, female $0.4 \times 0.6\text{--}0.8$ mm in internal diameter.

Gastrozooids squat and clavate, with 5–8 short tentacles attached about midway down the polyp. Dactylozooids adnate with only a tiny free part. Nematocysts of gastrozooid tentacles and dactylozooids measure about $6 \times 2 \mu\text{m}$; there are larger nematocysts ($9 \times 2.5 \mu\text{m}$) in the epidermis, but unfortunately a surface papilla was not sectioned.

Discussion.—Three species are assigned to *Stylantheca*, all endemic to shallow water in the northeastern Pacific. *S. porphyra* is most similar to *S. petrograpta* (Fisher, 1938), the latter differentiated only by its lower number of gastrozooids per cyclosystem (range 1–3, average 1.35 for the type-specimens), fewer dactylozooids per cyclosystem (range 4–9, average 5.8), and smaller cyclosystems (0.73–0.77 mm in diameter). The fewer gastrozooids and dactylopores per cyclosystem can probably be attributed to the smaller size of the cyclosystem, which, in turn, may be environmentally controlled. Therefore, it is possible that *S. petrograpta* may be synonymized or reduced to a subspecies or forma of *S. porphyra*. Fritchman (1974) has studied the planula and early settlement of *S. petrograpta*. The third species, *S. papillosa* (Dall, 1884), is known only from the tiny type-specimen which contains only 28 complete cyclosystems. Each cyclosystem has but one gastrostyle; dactylopores per cyclosystem range from 3–5 (average = 4.0); and the asymmetrical cyclosystems measure 0.82–0.85 mm in diameter. Because of its encrusting mode and only one gastrostyle per cyclosystem, it lies intermediate between typical *Stylaster* (Group A) and *Stylantheca*, but based on its coenosteal texture, gastrostyle, and general aspect, *S. papillosa* is tentatively assigned to *Stylantheca*. Obviously more specimens are needed to correctly resolve its position.

Distribution.—Known only from the Monterey Bay area, California, 0–1+ m.

Types.—The holotype and 13 paratype colonies are deposited at the USNM (43018, 43019, 43276, 43277). Presumably another paratype is at the BM. The types of all three species have been examined by the author.

Calyptopora Boschma, 1968

Stylaster: Pourtalès, 1867: 115.

Stenohelia: Kent, 1870: 123 (part: *S. complanata*).

Stylaster (*Stenohelia*): Broch, 1936: 10, 81 (part: *S. (S.) complanatus*).

Calyptopora Boschma, 1968a: 102.

Diagnosis.—Colonies flabellate. Branches round to elliptical in cross section, sometimes posteriorly carinate; branch anastomosis may occur. Coenosteum reticulate-granular and white, bearing numerous small papillae (nematopores), especially on larger diameter branches. Cyclosystems unilinearly or sometimes slightly

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Figure 18. *Stylantheca porphyra* (A–I, syntypes from Carmel Bay, California): A, colony, $\times 1.1$; B, coenosteal surface with cyclosystems and papillae, $\times 15$; C, cyclosystem, $\times 36$; D, longitudinal fracture of a cyclosystem revealing two gastrostyles and several dactylostyles, $\times 36$; E, coenosteum bearing papillae, $\times 67$; F, reticulate coenosteal texture, $\times 270$; G, gastrostyle, $\times 93$; H–I, dactylostyle and dactylostyle elements, $\times 144$, $\times 1,190$, respectively.

sympodially arranged, but in both cases the cyclosystems are all on the anterior side. Cyclosystems usually have one or more diastemas and one or more fixed lids of variable size. The lids are broad, tongue-shaped projections or simply the overdevelopment of several adjacent pseudosepta which overhang the gastropore. Lids are predominantly abcauline. Gastropores broad and deep with a small gastrostyle chamber containing a lanceolate, ridged gastrostyle of small-medium H:W. A ring palisade is present. Dactylostyles well developed. Ampullae superficial, sometimes with an efferent duct.

Discussion.—*Calyptopora* is very similar to *Stylaster* (Group C), differing primarily in its exclusively anterior facing and usually unilinearly arranged cyclosystems, and its cyclosystem lids. These character states are approached by various species of *Stylaster*: e.g., some species of *Stylaster* have two rows of anterolaterally arranged cyclosystems indicating a distinct anterior side, and the pseudosepta of *S. alaskensis* are sometimes strongly exsert, approximating a lip. Nonetheless, the three species now placed in *Calyptopora* are considered as a distinct genus.

Occurrence.—Recent: New Zealand region and northern Caribbean. 183–2,010 m.

Type Species.—*C. reticulata* Boschma, 1968, by original designation.

Calyptopora reticulata Boschma, 1968

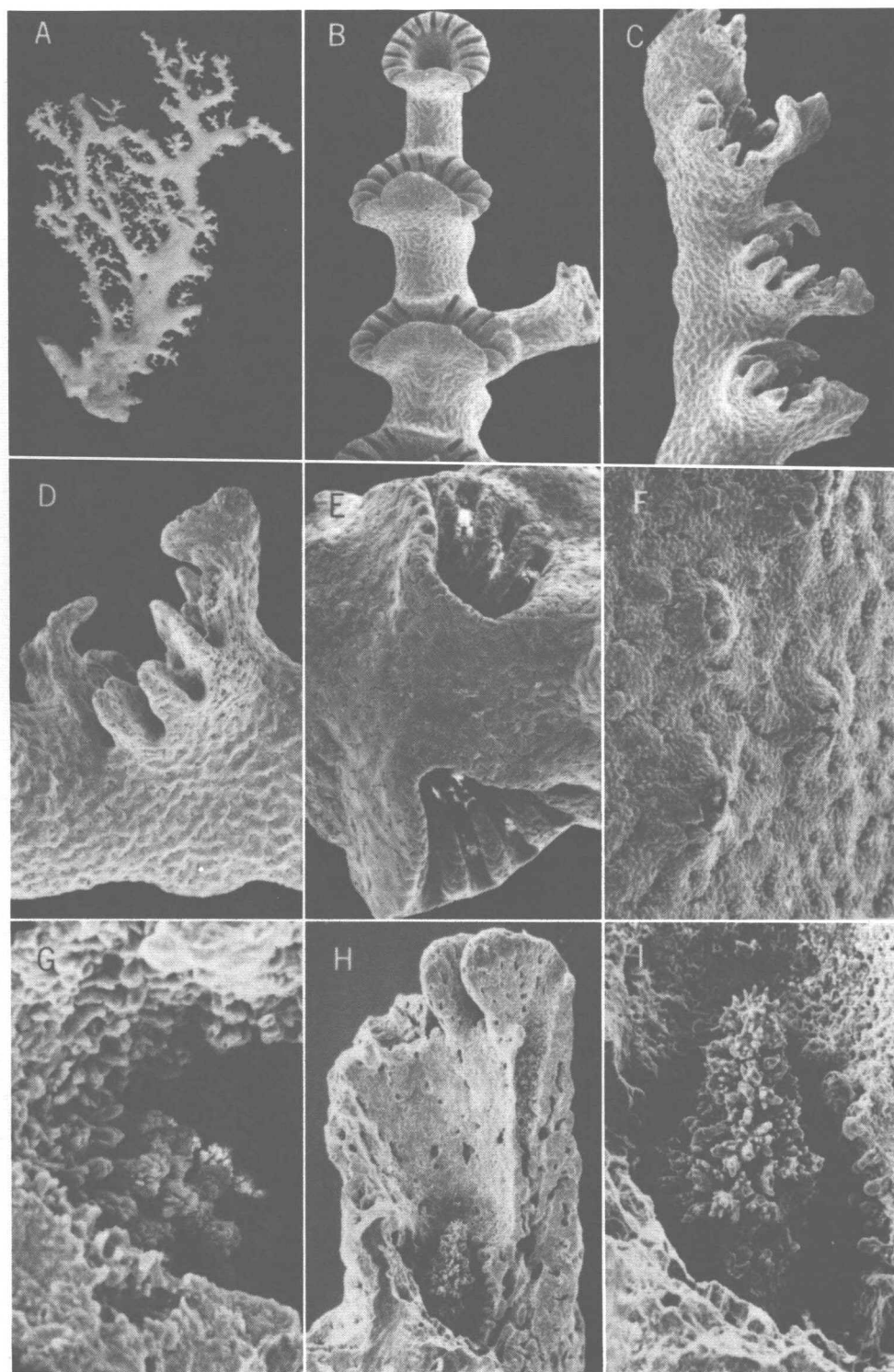
Figure 19A–I

Calyptopora reticulata Boschma, 1968a: 102–108, pls. 1–3, text-figs. 1–2; 1968c: 315–320 (in text).—Cairns, in press: figs. 41E, 49A–H, 50A–E.

Diagnosis.—Colonies large, up to 17 cm tall and 20 cm broad; basal branches up to 2.3×1.9 cm in diameter. Distal branches often have a continuous ridge along their posterior sides; larger diameter branches round to slightly elliptical in cross section and frequently anastomotic, producing a well reinforced flabellum. A commensal polychaete, *Malmgreniella dicirra* Hartman (identified by M. H. Pettibone), induces flattened calcareous tubes to be formed on both the anterior and posterior colony faces. Coenosteal strips 50–90 μ m broad, covered by irregularly shaped, angular granules. Nematopore mounds 0.14–0.20 mm in diameter and about 0.05 mm tall, each apically perforated with irregular slits. Cyclosystems 0.9–1.6 mm in diameter; one or two short diastemas often present on the adcauline perimeter of the cyclosystem, usually adjacent to an ascending branch. Pseudosepta often highly exsert, those on abcauline side often fused into a broad lid which overhangs the cyclosystem. Expression of lid quite variable, ranging from slightly overdeveloped pseudosepta to two broad lids (one ab- and one adcauline), which fuse over the cyclosystem, forming a canopy. Three to 17 dactylopores per cyclosystem; of 16 cyclosystems examined from the penultimate position on distal branches, the average was 11.3 ($\sigma = 2.27$), mode = 9.5. Gastrostyles up to 0.33 mm tall and 0.14 mm in diameter (H:W = 1.3–2.9). Dactylostyles consist of two to three adjacent rows of closely spaced pillars, measuring about 24 μ m tall by

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Figure 19. *Calyptopora reticulata* (A, E, Eltanin-1851: 49°40'S, 178°53'E, 476–540 m, 3 Jan. 1967; B, F, H–I, Eltanin-1991: 54°39'S, 170°22'E, 1,860–1,940 m, 2 Jan. 1968; C–D, G, Eltanin-2143: 49°51'S, 178°35'E, 2,010–2,100 m, 26 Feb. 1968): A, colony, $\times 0.43$; B–C, distal branch showing cyclosystem lids, $\times 14$; D, cyclosystem with lid, $\times 28$; E, cyclosystem with lids completely fused over gastropore, $\times 38$; F, coenosteal papillae, $\times 73$; G, dactylostyle, $\times 390$; H–I, cross section of gastrostyle chamber containing a gastrostyle, $\times 43$, $\times 133$, respectively.



16 μm in diameter. Female ampullae 0.65–1.06 mm in diameter, sometimes with a short, tubular, lateral efferent duct. Male ampullae 0.49–0.61 mm in diameter, often clustered on the outside of the worm tube.

The soft parts were poorly preserved in the specimen sectioned; however, the tiny gastrozooids have several tentacles and the dactylozooids are adnate. Nematocysts measuring $7 \times 2.5 \mu\text{m}$ are common in gastrozooid tentacles and dactylozooids.

Discussion.—Two other species are placed in *Calyptopora*. *C. complanata* was previously assigned to *Stenohelia*, but with the establishment of *Calyptopora* for the unifacial stylasterines with gastrostyles and fixed lids (Boschma, 1968a), and the added fact that *Calyptopora* does have dactylostyles (Cairns, in press), it becomes clear that *C. complanata* belongs in this genus. Examination of the types of both *C. complanata* and *C. virginis* show them to be synonymous, as Broch (1936) suspected. *C. pachypoma* (Hickson and England, 1905) is quite different from the other two species in coenosteal texture, gastropore shape, and lack of dactylostyles and should probably form the basis of a new genus.

Distribution.—Macquarie Ridge; New Zealand Plateau; off Antipodes, Bounty, and Chatham Islands. 349–2,010 m.

Types.—The holotype and some paratypes are deposited at the New Zealand Oceanographic Institute; other paratypes are at the RMNH (Vervoort and Zibrowius, 1981: 30). Types not examined by the author.

Stenohelia Kent, 1870

Allopora: Johnson, 1862: 196 (part).

Stenohelia Kent, 1870: 121.—Moseley, 1881: 97.—Boschma, 1956: F100; 1964b: 64–72.

Stylaster (*Stenohelia*): Hickson and England, 1905: 8, 15.—Broch, 1936: 10 (part: not *S. (S.) complanatus*).

Stylaster: Hickson and England, 1905: 13–16 (part).

Diagnosis.—Colonies flabellate and delicate; distal branches round in cross section and usually very thin, sometimes half the diameter of a cyclosystem in thickness. Sometimes polychaete commensals induce perforated tubes to be produced, which usually leads to a more robust and slightly bushy corallum. Coenosteum white and usually longitudinally ridged, especially on distal branches; larger diameter branches are either ridged or reticulate in texture. Usually the coenosteum is covered by irregularly shaped granules but in one case (*S. robusta*) a linear-imbricate texture is present. Nematopores often occur on the outside of worm tubes but are otherwise rare; coenosteal spines sometimes present. All cyclosystems originate on the anterior side and project perpendicular to the branch. Cyclosystems are usually unilinearly arranged on a branch and measure 0.8–2.0 mm in diameter. Gastropores very long and invariably curved 90° along the branch axis, sometimes extending all the way to the wall of the more proximal cyclosystem. In the latter case, the gastrostyle is not visible from the outside; however, usually the gastropore is shorter and the tip of the style can be glimpsed projecting through a well-developed ring palisade. Gastrostyle of medium to high H:W, irregularly ridged, and bears fused spines. Seven to 20 dactylopores per cyclosystem; no diastemas or lids. Dactylostyles rudimentary. Ampullae superficial hemispheres, usually clustered around a cyclosystem, but may also be scattered irregularly over the anterior and posterior surfaces.

Discussion.—*Stenohelia* is most similar to *Stylaster* (Group C), differing from it by having: (1) all cyclosystems on the anterior side, (2) a curved gastropore, (3)

slightly concave upper edges of the pseudosepta, and (4) ampullae clustered around the base of the cyclosystems.

Occurrence.—Western Pacific, Antipodes, Galapagos, Madeira, Cape Verde Islands, Lesser Antilles. 91–1,901 m.

Type Species.—*Allopora maderensis* Johnson, 1862, by subsequent designation (Broch, 1936: 8).

Stenohelia maderensis (Johnson, 1862)

Figure 20A–B, D–G

Allopora maderensis Johnson, 1862: 196–197, text-figs. 1–3.—Boschma, 1956: F100.

Stenohelia maderensis: Kent, 1870: 121–122; 1871: 277, pl. 24, fig. 3.—Boschma, 1957: 31–32; 1967: 325–329 (part: pl. 1, figs. 2–4, pl. 2, figs. 3–4, not specimens from St. Vincent).—Zibrowius and Cairns, 1982: 211–212.

Allopora madeirensis: Studer, 1878: 633.

Stenohelia madeirensis: Moseley, 1881: 88.—Greeff, 1886: 21.

Stylaster tiliatus: Hickson, 1912b: 461–462.

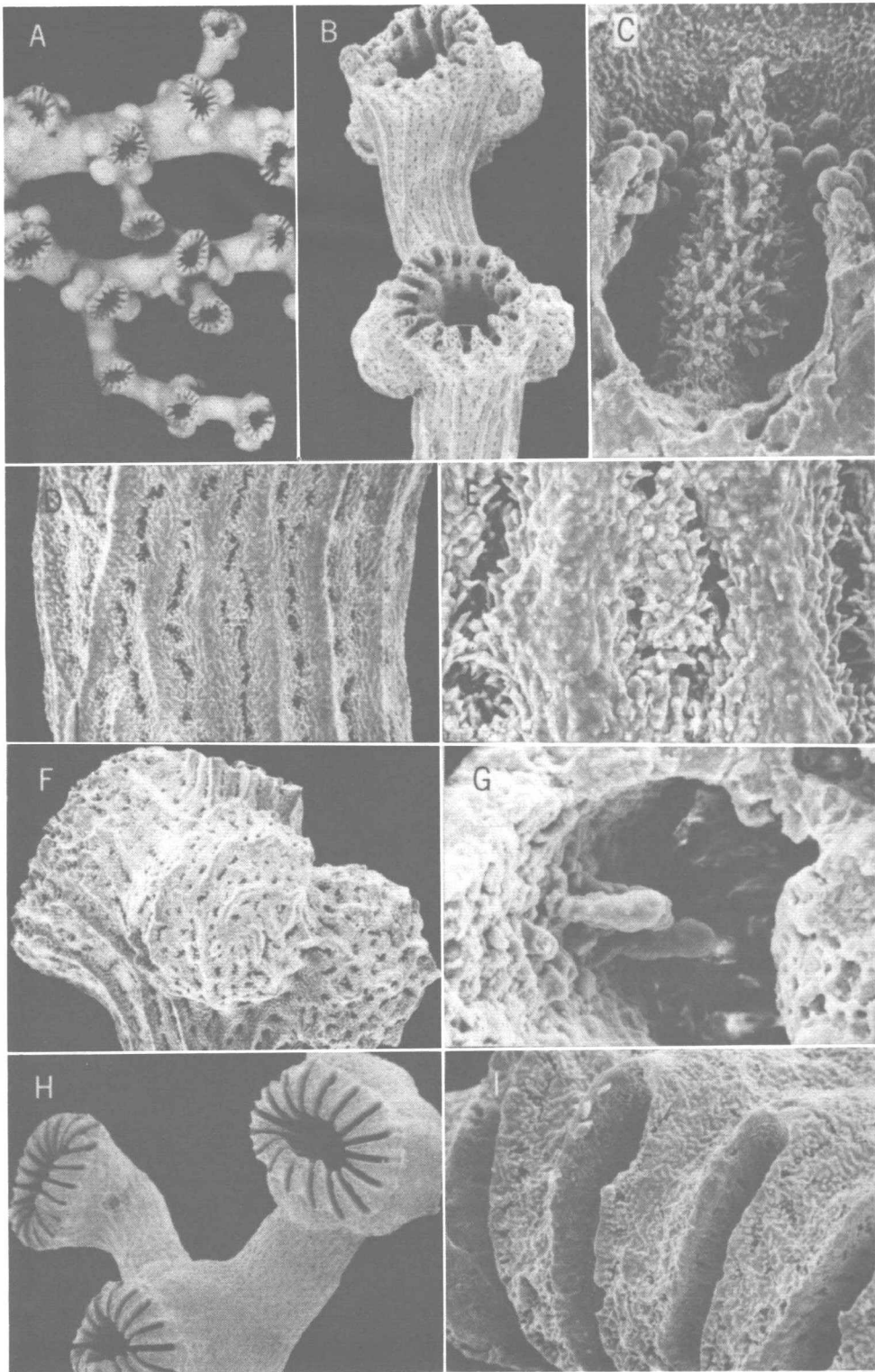
Not *Stenohelia maderensis* Boschma, 1964b: 64–69, pl. 1, figs. 13–14 (= *S. profunda*); 1964c: 80–84, pl. 2 (= *S. profunda*).

Diagnosis.—Colonies up to 9 cm tall and 5.7 cm broad, supported by a basal branch up to 5 mm in diameter. Branches anastomose infrequently and there is no polychaete commensal. Coenosteal strips 75–85 μm wide and usually slightly convex to ridged; sometimes ridged strips alternate with flatter ones. Coenosteal slits deep, about 10 μm wide. Strips covered by slender, rudimentary, imbricated scales. Cyclosystems elliptical in cross section, about 1.0 mm in greater diameter and 0.8 mm in lesser, the greater diameter transverse to the branch. Gastrostyles lanceolate, about 0.4 mm tall and 0.16 mm in diameter (H:W = 2.5), the tip easily visible from the outside. Ring palisade well developed. Of 100 cyclosystems examined, Boschma (1967) found a range of 9–19 dactylopores per cyclosystem, average = 13.5, and mode = 14. Dactylostyles composed of a unilinear row of slightly clavate elements about 42 μm tall and 12 μm in diameter. Ampullae quite prominent, expressed as globose hemispheres 0.75–0.85 mm in diameter surrounding the cyclosystems, and also sometimes found on the posterior side of the branch opposite a cyclosystem. Ampullae warty and often ridged. Female efferent ducts are indicated by a shallow circular depression about 0.17 mm in diameter on the sides of each ampulla.

Alcohol-preserved specimens of *S. maderensis* were not available for study, but examination of the soft parts of the closely related *S. profunda* from ALBATROSS-2753 (Figs. 20C, H–I, 24D, 26E, 27E–F) revealed a robust, cylindrical gastrozoid about 0.5 mm tall with a whorl of seven tentacles below an extended hypostome. Dactylozooids adnate. Nematocysts measuring 5.0–5.5 \times 2.0–2.5 μm common in gastrozoid tentacles and dactylozooids.

Discussion.—Ten species are assigned to *Stenohelia* (Table 1), only two of which occur in the Atlantic. *S. maderensis* is distinguished from the western Atlantic *S. profunda* Moseley, 1879, by its smaller, more regularly shaped cyclosystems; less dactylopores per cyclosystem; larger, more conspicuous ampullae; coarser coenosteal ridges; and shorter gastropore, which allows the gastrostyle tip to be seen from the outside. Boschma's (1964b; c; 1967) records of *S. maderensis* from the West Indies are *S. profunda*.

Stenohelia boschmai Wells, 1977 (Eocene, Tonga), is removed from *Stenohelia* and placed incertae sedis. Wells (1977) did not observe gastrostyles in his specimens and examination of his material suggests that gastrostyles were never pres-



ent. *S. boschmai* has the appearance of a *Crypthelia* without lids. No currently defined genus is appropriate to receive *S. boschmai*.

Distribution.—Known only from Madeira and Cape Verde Islands. 91–275 m.

Types.—The holotype was originally deposited at the BM but can no longer be found there; it is presumed to be lost.

Conopora Moseley, 1879

Stylaster: Studer, 1878: 635 (part).

Conopora Moseley, 1879: 503; 1881: 97.—Hickson and England, 1905: 25.—Broch, 1936: 84–87.—Boschma, 1956: F100.

Group A

Diagnosis.—Colonies flabellate unless modified by a commensal polychaete, which induces a somewhat bushy and more robust growth form. Distal branches delicate and slightly compressed in the plane of the colony, supporting sympodially arranged cyclosystems in alternating positions on the lateral branch edges; larger branches sometimes anastomose. Coenosteum irregularly linear-imbricate, covered by broad, flat platelets. Raised nematopores often present, sometimes in great density, especially on larger branches, the exterior of worm tubes, and the tops of pseudosepta. Coenosteum white. Distal cyclosystems slightly exsert and oriented toward the branch tip, as in *Stylaster* (Group C). Gastropore consists of two chambers, the upper, larger chamber separated from the lower, thinner one by a constricted aperture analogous (? homologous) to the ring palisade. Adcauline diastemas common in some species. Dactylotomes extend deeply into upper gastropore chamber. No gastro- or dactylostyles. Female ampullae usually superficial; male ampullae usually internal, communicating with the upper gastropore chamber via an efferent duct.

Group B

Diagnosis.—Colonies robust; branches large and round in cross section, supporting randomly arranged cyclosystems on all branch surfaces, as in *Stylaster* (Group A). Coenosteum reticulate-granular; nematopores common. No polychaete commensalism observed. Otherwise, similar to Group A.

Discussion.—*Conopora* is remarkably similar to *Stylaster*, differing primarily by its absence of gastro- and dactylostyles. Both genera even have a broad range of colony shapes and cyclosystem arrangement, which created the need for similar groups within the genera: *Stylaster* (Group A) and *Conopora* (Group B) are equivalent and *Stylaster* (Group C) and *Conopora* (Group A) are equivalent. *Stylaster* (Group B), the annectant group, has no counterpart in *Conopora*; however, it is interesting to note that two of the several hundred colonies of *C. verrucosa* examined had cyclosystems scattered irregularly on all sides of several distal branch-

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Figure 20. *Stenohelia maderensis* (A–B, D–G, specimens from Santiago de la Praya, Cape Verde Islands, BM 1950.1.11.81): A, part of colony, $\times 3.8$; B, F, branch fragment with ampullae, $\times 20$, $\times 40$, respectively; D–E, coenosteal texture, $\times 83$, $\times 270$, respectively; G, dactylostyle, $\times 400$. *Stenohelia profunda* (C, H–I, Albatross-2753: $13^{\circ}34'N$, $61^{\circ}03'W$, 514 m, 4 Dec. 1887): C, gastrostyle and ring palisade, $\times 100$; H, cyclosystem and ampullae around base of cyclosystem, $\times 13$; I, pseudosepta of a cyclosystem, $\times 100$.

es, possibly indicating a similar transition within *Conopora*. In *Stylaster*, the groups were historically given separate generic names, but not in *Conopora*, an inconsistency noted by Boschma (1968a: 101). However, the inconsistency is circumvented by considering *Stylaster* as a genus with three groups and *Conopora* as a genus with two groups.

Occurrence.—Group A: Recent: Indo-West Pacific, Antarctic and Subantarctic, New Zealand. 110–2,355 m.—Group B: ?Paleocene: Denmark; Recent: Providence, Indian Ocean. 228 m.

Type Species.—*C. tenuis* Moseley, 1879 (= *Conopora laevis* (Studer, 1878)), by monotypy.

Conopora laevis (Studer, 1878)

Figure 21A–D

Stylaster laevis Studer, 1878: 635, pl. 2, fig. 5a–b.—Not Moseley, 1881: 81 (= *C. verrucosa*).—Boschma, 1957: 12.

Stylaster obliquus Studer, 1878: 635–636, pl. 2, fig. 7a–d.

Conopora tenuis Moseley, 1879: 503; 1881: 82, pl. 12, figs. 5a–b, 6.—?Hickson and England, 1905: 25; 1909: 351.—?Broch, 1936: 88–91, pl. 13, fig. 37.—Boschma, 1956: F100, fig. 82, 2a; 1957: 39; 1966: 115–116.

Stenohelia obliqua: Boschma, 1957: 32.

Conopora laevis: Zibrowius, 1981: 274–277, pl. 3, figs. 8–11, pl. 4, figs. 1–5.

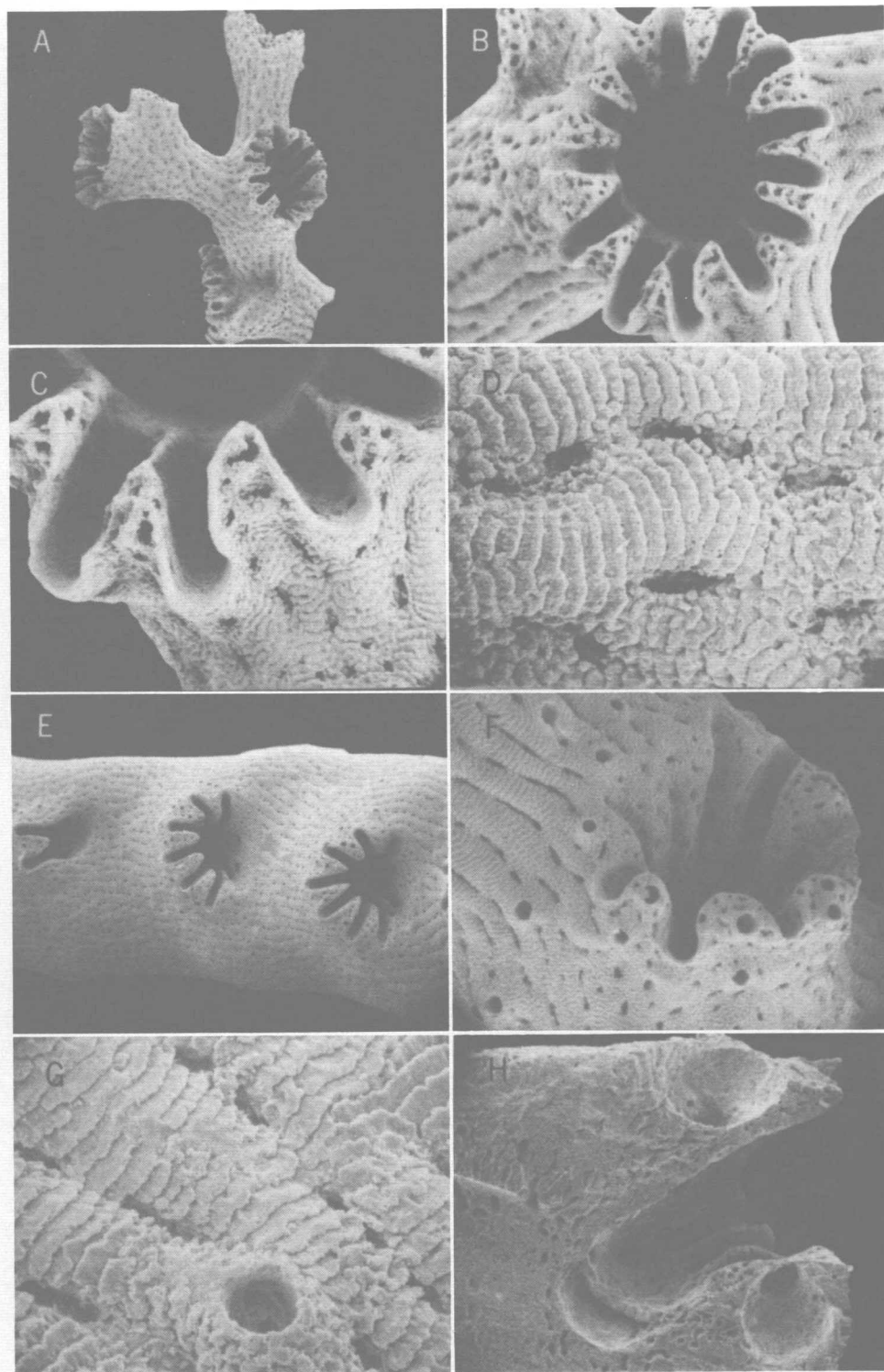
Diagnosis.—Colonies up to 6.5 cm tall with a basal branch diameter up to 5.5 mm. Coenosteal strips 62–115 μ m wide, covered by equally broad, imbricated platelets with a frequency of 55–60 leading edges per mm. The free edges of the platelets are usually directed toward the branch tip, but occasionally a series is directed proximally, and at some point on the coenosteal strip the series meet with little disruption. No nematopores. Cyclosystems round to elliptical, 1.02–1.22 mm in greater diameter; no diastemas. Based on 19 cyclosystems from the holotype of *C. laevis*, the range of dactylopores per cyclosystem is 8–12, average = 10.0 ($\sigma = 1.52$). Dactylotomes are about 0.1 mm wide; pseudosepta are wedge shaped and sometimes concave. Male ampullae internal; female ampullae superficial, up to 0.6 mm in diameter. Soft parts unknown.

Discussion.—Only five species are assigned to *Conopora* (Table 1). I have examined the types of all but one of the nominal species (*C. major*) and herein synonymize *C. pauciseptata* Broch, 1951 with *C. verrucosa* (Studer, 1878) and strongly doubt the placement of *C. arborescens* Nielsen, 1919, in this genus. The poor preservation of a syntype and topotypic specimen of *C. arborescens* does not allow a decision on whether or not the cyclosystems have gastrostyles; in this case, *Stylaster* (Group A) cannot be ruled out.

C. laevis is most similar to *C. verrucosa*, but can be distinguished by its complete lack of nematopores, lack of cyclosystem diastemas and thus having slightly more

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Figure 21. *Conopora laevis* (A–D, syntype of *C. tenuis* from Challenger-170: 29°55'S, 178°14'W, 951 m, 14 July 1874, BM 1880.11.25.184): A, distal branch, $\times 14$; B, cyclosystem, $\times 41$; C, pseudosepta, $\times 80$; D, imbricate coenosteal texture, $\times 167$. *Conopora verrucosa* (E, Edisto 14-2: 71°50'S, 15°50'W, 1,006–1,189 m, 18 Jan. 1959; F–G, Vema 17-61: 54°44'S, 55°39'W, 1,814–1,919 m, 11 May 1961; H, Eltanin-1089: 60°47'S, 53°30'W, 641 m, 17 Apr. 1964): E, branch segment showing reduction in number of dactylopores per cyclosystem from distal to proximal end, $\times 14$; F, cyclosystem and nematopores, $\times 47$; G, imbricate coenosteal texture and nematopores, $\times 200$; H, longitudinal section through a cyclosystem flanked on either side by internal ampullae, $\times 27$.



dactylopores per cyclosystem, more exsert cyclosystems, and more widely separated cyclosystems. The nematopores of *C. verrucosa* are sometimes very dense (separated from one another by only 1–3 diameters), tall (up to 0.15 mm), and distributed over the entire colony. The type of *C. verrucosa* is a specimen such as this. However, the nematopores may also be much less common (occurring only on the pseudosepta and worm tube), and flush with the coenosteum. The type of *C. pauciseptata* and most of the specimens reported by Cairns (in press) as *C. pauciseptata* are intermediate between these extremes. *C. verrucosa* is also characterized by adcauline diastemas, not on distal cyclosystems but on those cyclosystems of larger diameter branches. The diastema reduces the average number of dactylopores per cyclosystem to about 7.1 (Boschma, 1966). Finally, the cyclosystems on basal branches of *C. verrucosa* are flush or almost sunken into the coenosteum and the cyclosystems on distal branches are more crowded.

Soft tissue of *C. laevis* was not available for study, but tissue of *C. verrucosa* from Edisto TD 2-14 (Figs. 21E–H, 26A, H) revealed a compressed hemispherical gastrozoid occupying the lower gastropore chamber which led via a narrow neck to a mound-like hypostome. Instead of tentacles, the hypostome contains large inflated cells. Dactylozooids adnate. Nematocysts of nematophores about $29 \times 4 \mu\text{m}$; smaller nematocysts measuring about $8 \times 1.2 \mu\text{m}$ are less common in the tissue.

Distribution.—Off New Zealand, Chatham Island, Kermadec Islands, ?Indonesia, ?Chagos Archipelago, ?western Indian Ocean, ?Japan. 110–951 m. (The distributional records of Hickson and England (1905, 1909) and Broch (1936) have not been verified.)

Types.—The types of *S. laevis* and *S. obliquus* are deposited at the Zoologisches Museum, Berlin (1776, 1778, respectively). The syntypes of *C. tenuis* are deposited at the BM (1880.11.25.184). All of these types were examined by the author.

Crypthelia Milne Edwards and Haime, 1849

Crypthelia Milne Edwards and Haime, 1849: 69.—Broch, 1936: 93–95.—Boschma, 1951: 455–456; 1956: F100.

Endhelio Milne Edwards and Haime, 1849: 69.

Cryptohelia Milne Edwards and Haime, 1857: 127.—Moseley, 1881: 98.—Hickson and England, 1905: 20.

Endohelia Milne Edwards and Haime, 1857: 128.

Diagnosis.—Colonies flabellate and usually small and delicate. About one-quarter of the species are associated with a commensal polychaete, which induces a more robust colony. Branches round in cross section and very thin; distal branches thinner in diameter than the cyclosystems they support. Coenosteum linear-imbricate on distal branches, although this pattern is sometimes obscured on basal branches; coenosteum white. Nematopores common on coenosteum, particularly on the lid and pseudosepta. All cyclosystems originate on the anterior side of the colony except in *C. trophostega*, which is bifacial; cyclosystems project at right angles to the branch. Cyclosystems round to elliptical in cross section, ranging from 0.7–5.0 mm in diameter. Gastropore composed of two chambers, the lower one very reduced. Every cyclosystem bears a fixed lid, usually attached at the abcauline position, which overhangs the gastropore to a variable degree. In the most extreme cases, the lid fuses to the coenosteum on the adcauline side, almost completely covering the cyclosystem and allowing the polyp to feed through only two lateral slits. Multiple lids are sometimes present. Seven to 25 dactylopores per cyclosystem; tops of pseudosepta often concave. No gastro- or dactylostyles.

Ampullae superficial and large, usually associated with the lid or encircling the cyclosystem. Efferent ducts from both male and female ampullae open into the cyclosystem.

Discussion.—Among the three genera of Stylasterinae that do not have gastrostyles, *Crypthelia* is easily distinguished by its prominent lids, which cover all or part of the cyclosystem. It is most similar to *Astya*, which has an homologous structure much lower in the gastropore chamber.

Occurrence.—Eocene: Tonga; Recent: Atlantic, Indo-West Pacific, North Pacific, Galapagos, off Panama (Pacific), Subantarctic. 183–2,789 m.

Type Species.—*Crypthelia pudica* Milne Edwards and Haime, 1849, by monotypy.

Crypthelia pudica Milne Edwards and Haime, 1849
Figure 22A–H

Crypthelia pudica Milne Edwards and Haime, 1849: 69; 1850: 93, pl. 3, fig. 1.—Broch, 1936: 95–99, pl. 13, fig. 39, text-fig. 31.—Boschma, 1956: F100; 1957: 36–38 (synonymy).—?Eguchi, 1965: 219, text-figs. 1–3.

Cryptohelia pudica: Milne Edwards and Haime, 1857: 127.—?Moseley, 1881: 71–76, 82–83 (Not CHALLENGER sta. 3, 24, and 236, but perhaps sta. 171).—?Alcock, 1899: 11.—Hickson and England, 1905: 21.—Fisher, 1938: 535, pl. 64, fig. 1.—?Naumov, 1960: 588–590, text-figs. 434–435.

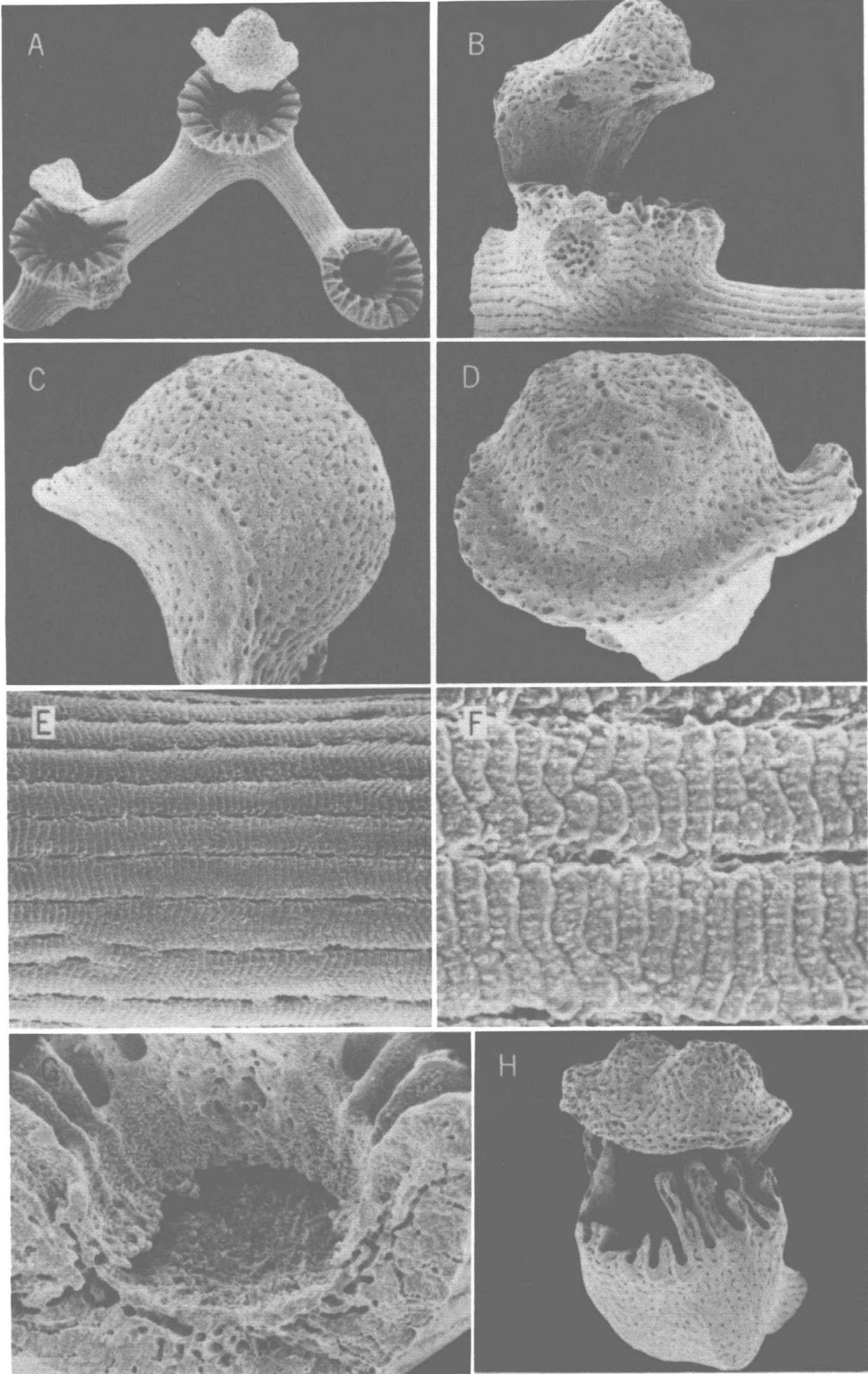
Not *Cryptohelia pudica*: Studer, 1878: 633–634.—Marenzeller, 1904: 86.

Diagnosis.—Colonies very delicate, up to 7 cm tall; basal branches up to 2.2 mm in diameter. Coenosteal strips about 70 μ m wide; platelets equally broad, about 75 per mm. Nematopores, about 40–45 μ m in diameter, are restricted to the lids and pseudosepta. Cyclosystems round to slightly elliptical in cross section, 1.2–1.5 mm in diameter; 15–19 dactylopores per cyclosystem. Thin, lower chamber of gastropore spiny, separated from upper chamber by a ring palisade instead of a solid, annular constriction. Lid large, covering the entire cyclosystem; lid raised high above the gastropore as a horizontal canopy; top of lid slightly concave. Female ampullae large, superficial hemispheres up to 1.3 mm in diameter and 1.1 mm tall, occurring on the top of each lid, usually one per lid. Male ampullae much smaller hemispheres, about 0.55 mm in diameter, occurring in clusters of 3–5 on the tops of lids. Immature cyclosystems have no ampullae and their lids are very thin, as illustrated by Milne Edwards and Haime (1850). Both male and female ampullae have efferent ducts (pores) visible on the lower side of the lid, one pore corresponding to each ampulla.

Soft tissue of *C. pudica* was not available for study; however, examination of tissue from an undescribed species from the Galapagos (Figs. 26F, 28B) revealed a crescent-shaped gastrozoid without tentacles, adnate dactylozooids with a long free part, and nematocysts measuring $20 \times 2.5 \mu$ m in the nematophores and 7×2.0 – 2.5μ m in the dactylozooids. Moseley (1881) and Broch (1947) also reported gastrozooids without tentacles for other species of *Crypthelia*, and the former described the soft parts of *C. affinis* in great detail.

Discussion.—The 15 species of *Crypthelia* (Table 1) are differentiated primarily on the basis of cyclosystem diameter, size and shape of the lid, and size and position of the ampullae. *C. pudica* is characterized by relatively small cyclosystems with large lids and very conspicuous ampullae restricted to the top of the lid.

The type-specimen of *C. pudica* could not be obtained from the MNHNP and is presumed to be lost. My diagnosis and most figures for this species are based



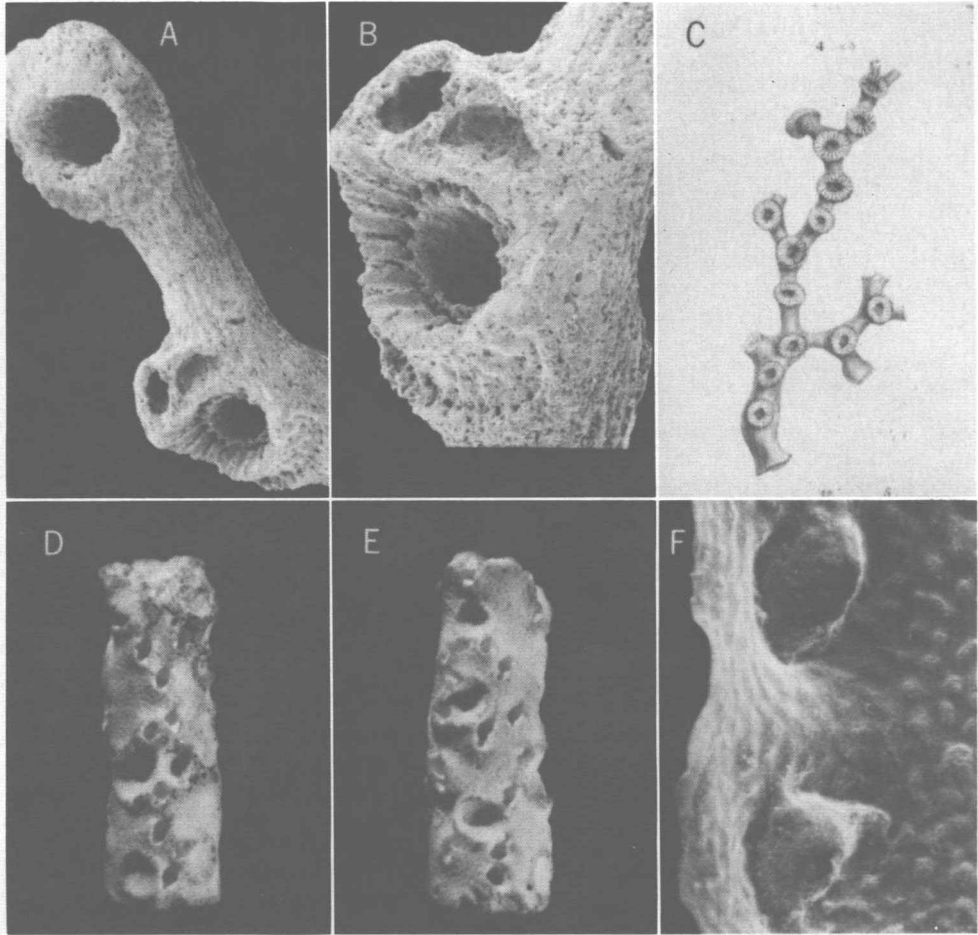


Figure 23. *Astya nielsenii* (A–B, paratype): A, branch segment, $\times 14$; B, enlargement of a cyclosystem, $\times 27$. *Astya subviridis*: C, copy of Moseley's (1881) pl. 1, fig. 4, $\times 2.1$. *Congregopora nasiformis* (D–E, figured syntype, MMH 1750; F, topotypic specimen): D–E, branch segment, $\times 3.2$; F, ?gastropores, $\times 27$.

on topotypic (*sensu lato*) specimens from ALBATROSS-5423 ($9^{\circ}38'N$, $121^{\circ}11'E$, 929 m), described and figured by Fisher (1938). They differ from the figured type in having conspicuous ampullae in their lids; however, it is suggested that the figures of Milne Edwards and Haime (1850) are those of immature cyclosystems before ampullae had formed.

Several of the synonymy entries are prefaced with a question mark because I

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Figure 22. *Crypthelia pudica* (A–H, Albatross-5423: $9^{\circ}38'N$, $121^{\circ}11'E$, 929 m, 31 Mar. 1909): A, branch fragment showing increasing development of female ampullae away from the tip, $\times 13$; B, male cyclosystem, efferent pores from ampullae in lid visible on underside of lid, $\times 30$; C–D, fully developed female ampulla, scattered nematopores, $\times 40$; E–F, imbricate coenosteal texture, $\times 83$, $\times 280$, respectively; G, longitudinal fracture through a cyclosystem showing flattened lower chamber, $\times 67$; H, aberrant male cyclosystem with highly developed pseudosepta, $\times 30$.

have not examined them; their distributional records are therefore also queried. Studer's (1878) specimen, however, was examined and found not to be *C. pudica* but an undescribed species similar to *C. fragilis*. Marenzeller's (1904) specimens (USNM 21285) also appear to be an undescribed species.

Distribution.—?Indian Ocean (368 m), Kermadec Island (1,097 m), Philippine Islands (549–1,633 m), ?Japan, ?Sea of Okhotsk (1,240 m).

Types.—Muséum National d'Histoire Naturelle, Paris (presumed lost). The types of 10 of the 15 species have been examined by the author.

Astya Stechow, 1921

Astylos Moseley, 1879: 457; 1881: 65, 97–98.

Astya Stechow, 1921: 253 (nom. nov.).—Boschma, 1956: F100.

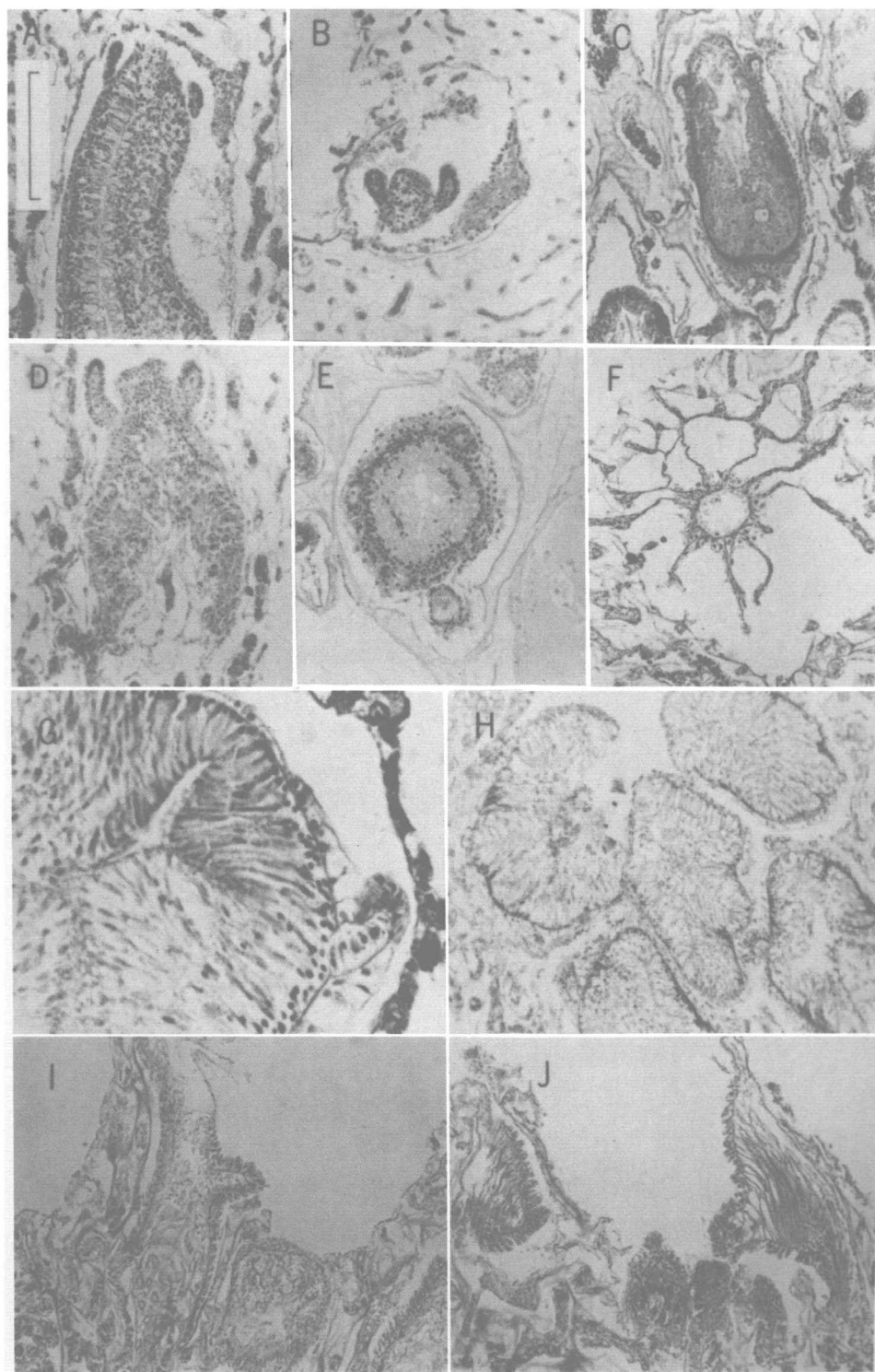
Diagnosis.—Colonies small, delicate, and flabellate. Branches round in cross section and very thin; distal branches usually thinner in diameter than the cyclo-systems they support. Coenosteum linear-imbricate, white. All cyclo-systems originate on the anterior side of the colony and project at right angles to the branch. Cyclo-systems slightly exsert, round to elliptical in cross section, up to 1.9 mm in greater diameter. Gastropore composed of two chambers, as in *Conopora* and *Cryptothelia*; however, in *Astya* a short, blunt pillar projects into the constricted aperture that separates the chambers. Seventeen to 19 dactylopores per cyclo-system. The upper, outer edge of each pseudoseptum bears a nematopore. No gastro- or dactylostyles. Ampullae restricted to a ring encircling the base of each cyclo-system, causing the cyclo-systems to appear globose.

The gastrozoid fills the crescent-shaped lower chamber and also projects upward as a cylindrical tube. Mouth cruciform, no tentacles. Dactylozoids are adnate with long free tentacles. Nematocysts of nematophores about $23 \times 6 \mu\text{m}$. Tissue bluish green.

Discussion.—Three genera (*Astya*, *Cryptothelia*, and *Conopora*) are characterized by having a double-chambered gastropore, prominent nematophores, and lacking gastro- and dactylostyles. *Astya* is most similar to *Cryptothelia* in that they are both unifacial, have superficial ampullae clustered around the cyclo-systems, and have a protective lid or small pillar covering the gastrozoid. They differ in that *Astya* has a small pillar overhanging only the gastrozoid, whereas *Cryptothelia* has a lid

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Figure 24. Histological sections of gastro- and dactylozoids: A, *Adelopora pseudothyron*, paratype from Eltanin 25–326: $46^{\circ}04'S$, $83^{\circ}55'W$, 298 m, 9 Oct. 1966, longitudinal section of gastrozoid including two tentacles; B, same specimen as figure A, oblique section through hypostome, two tentacles, and part of operculum; C, *D. (Haplomerismos) anceps*, paratype, longitudinal section through gastrozoid including two tentacles; D, *Stenohelia profunda*, Johnson-Smithsonian Deep-Sea Expt.-43: $18^{\circ}04'N$, $67^{\circ}48'W$, 439–549 m, 11 Feb. 1933, longitudinal section through gastrozoid including two tentacles; E, *Lepidotheca fascicularis*, paratype from Eltanin-1416: $53^{\circ}45'S$, $159^{\circ}09'E$, 787–842 m, 9 Feb. 1965, cross section of gastrozoid including four tentacles, larger canal at lower right is a coenosteal canal; F, *Sporadopora dichotoma*, Islas Orcadas 575-82: $55^{\circ}29'S$, $35^{\circ}20'W$, 413–462 m, 6 June 1975, cross section of radial canals and gastrozoid sac; G, *Pliobothrus symmetricus*, SABP, BLM-2H: $32^{\circ}20'N$, $78^{\circ}10'W$, 411 m, 15 Feb. 1977, cross section of gastrozoid including one tentacle; H, *Stylantheca porphyra*, topotypes from Carmel Bay, cross section through five gastrozoids in one cyclo-system; I, *Errinopora pourtalesii*, Albatross-3159: $37^{\circ}47'N$, $123^{\circ}10'W$, 49 m, 22 Mar. 1890, longitudinal section of gastrozoid flanked by adnate dactylozoid on left; J, *Gyropora africana*, BM specimen, gastrozoid flanked on either side by adnate dactylozoids. Scale bar for A–F, H–J = 0.2 mm (200 μm); G = 50 μm .



overhanging the cyclosystem. Moseley (1881) suggested that they were homologous structures but did not predict the polarity of the character states.

Occurrence.—Eocene: Tonga; Recent: off Meangis Islands, Philippines. 914 m.

Type Species.—*A. subviridis* Moseley, 1879, by monotypy.

Astya subviridis (Moseley, 1879)

Figures 23C, 28A

Astylus subviridis Moseley, 1879: 457–462, pl. 34, fig. 4, pl. 35, figs. 8, 15, pl. 41, fig. 1, pl. 43, figs. 10–11, pl. 44, fig. 2; 1881: 65–71, pl. 1, fig. 4, pl. 2, figs. 8, 15, pl. 8, fig. 1, pl. 10, figs. 10–11, pl. 11, fig. 2.

Astya subviridis: Stechow, 1921: 253.—Boschma, 1956: F100, fig. 82, 3; 1957: 40.

Diagnosis.—See that of genus.

Discussion.—There are two species in the genus *Astya*. Even though the preservation of the Eocene-aged *A. nielsenii* Wells, 1977 (Fig. 23A–B), is not good enough to see the characteristic tongue-like projection between gastropore chambers, there is little doubt that it belongs to *Astya*. On the other hand, the placement of *Astya crassa* (Nielsen, 1919) is quite uncertain. It has sympodially arranged cyclosystems and randomly placed ampullae; the preservation is not good enough to judge presence or absence of gastrostyles. It may be either a *Stylaster* (Group C) or a *Conopora*, but probably not *Astya*; it is therefore placed incertae sedis.

A. subviridis is apparently known from only one specimen, the figured type, deposited at the BM (1880.11.25.185), which, unfortunately, has almost completely disintegrated. Moseley's (1879) excellent description of both hard and soft parts forms the basis of our knowledge of this species. The only character I can add to Moseley's description is the imbricate nature of the coenosteum, barely visible on one fragment.

Distribution.—Off Meangis Islands, Philippines. 914 m.

Types.—Holotype at the BM (see Discussion). The types of all three nominal species have been examined by the author.

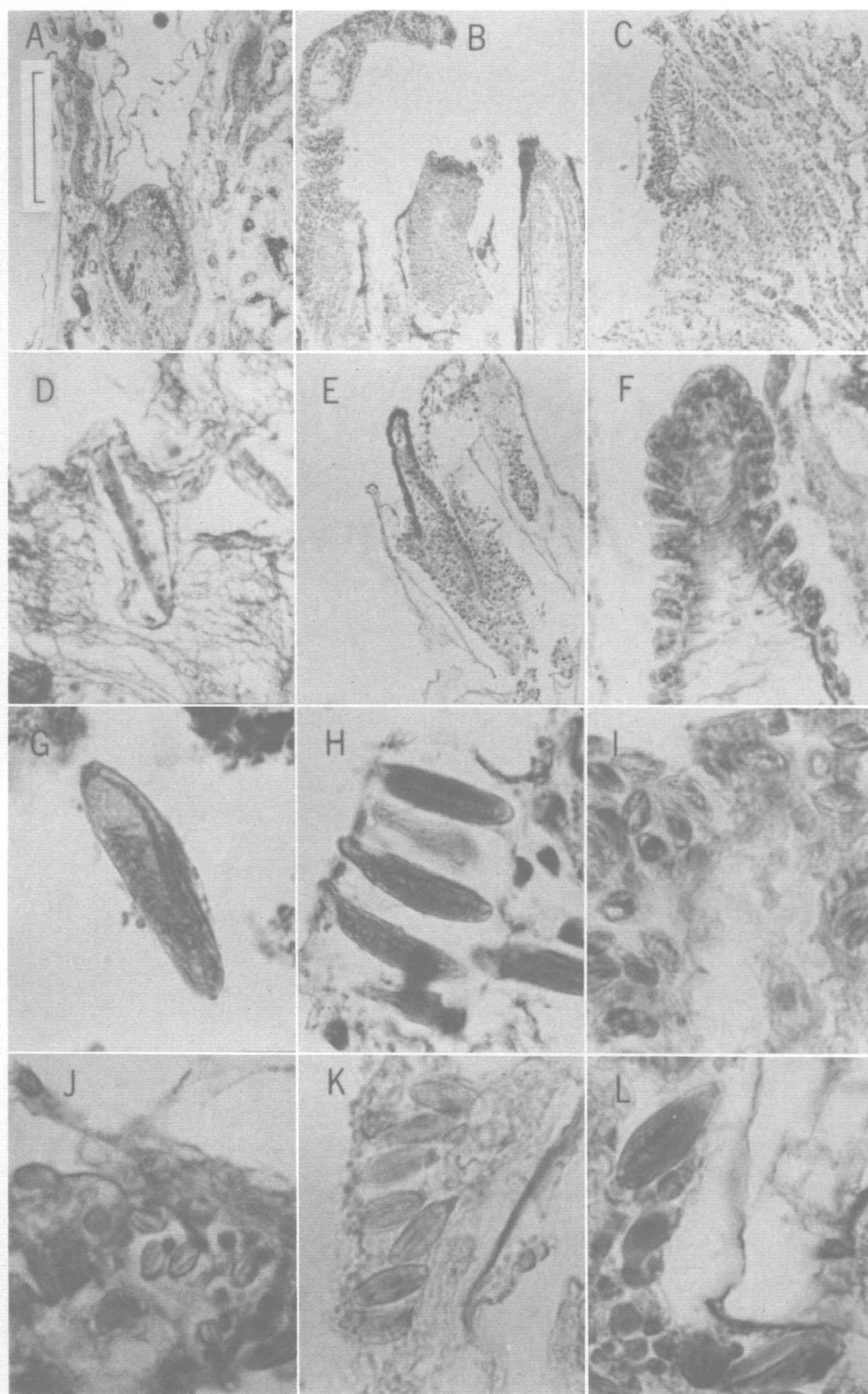
Incertae Sedis

Congregopora Nielsen, 1919

Congregopora Nielsen, 1919: 21.—Boschma, 1951: 39–42; 1956: F100.

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Figure 25. Histological sections of gastro- and dactylozooids, and nematocysts: A, *Stylaster roseus*, Carrie Bow Cay, longitudinal section through gastrozooid including one tentacle, and dactylozooids; B, *Inferiolabiata labiata*, Eltanin-1536: 54°29'S, 39°22'W, 659–686 m, 8 Feb. 1966, longitudinal section through gastrozooid flanked by one large, overhanging dactylozooid; C, *Errina antarctica*, Hero 715–874: 54°39'S, 63°50'W, 135–137 m, 26 Oct. 1971, adnate dactylozooid; D, *Phalangopora regularis*, type of *Pliobothrus seriatus*, simple dactylozooid; E, *Lepidotheca fascicularis*, paratype from Eltanin-1416: 53°45'S, 159°09'E, 787–842 m, 9 Feb. 1965, dactylozooid; F, *D. (Haplomerismos) anceps*, paratype, tip of dactylozooid; G, *Pliobothrus symmetricus*, SABP, BLM-2H: 32°20'N, 78°10'W, 411 m, 15 Feb. 1977, USNM 49130, nematocyst in a coenosteal canal; H, *Sporadopora dichotoma*, Islas Orcadas 575-82: 55°29'S, 35°20'W, 413–462 m, 6 June 1975, nematocyst of a nematophore; I, *Stelapora echinata*, Eltanin-1593: 54°43'S, 56°37'W, 339–357 m, 14 Mar. 1966, nematocyst of a dactylozooid; J, *Phalangopora regularis*, type of *P. seriatus*, nematocysts; K, *Errinopora pourtalesii*, Albatross-3159: 37°47'N, 123°10'W, 49 m, 22 Mar. 1890, cluster of nematocysts in coenosteum near gastropore; L, *Gyropora africana*, BM specimen, nematocysts. Scale bar for A–C, E = 200 µm; D, F = 50 µm; H = 41 µm; G, I–L = 20 µm.



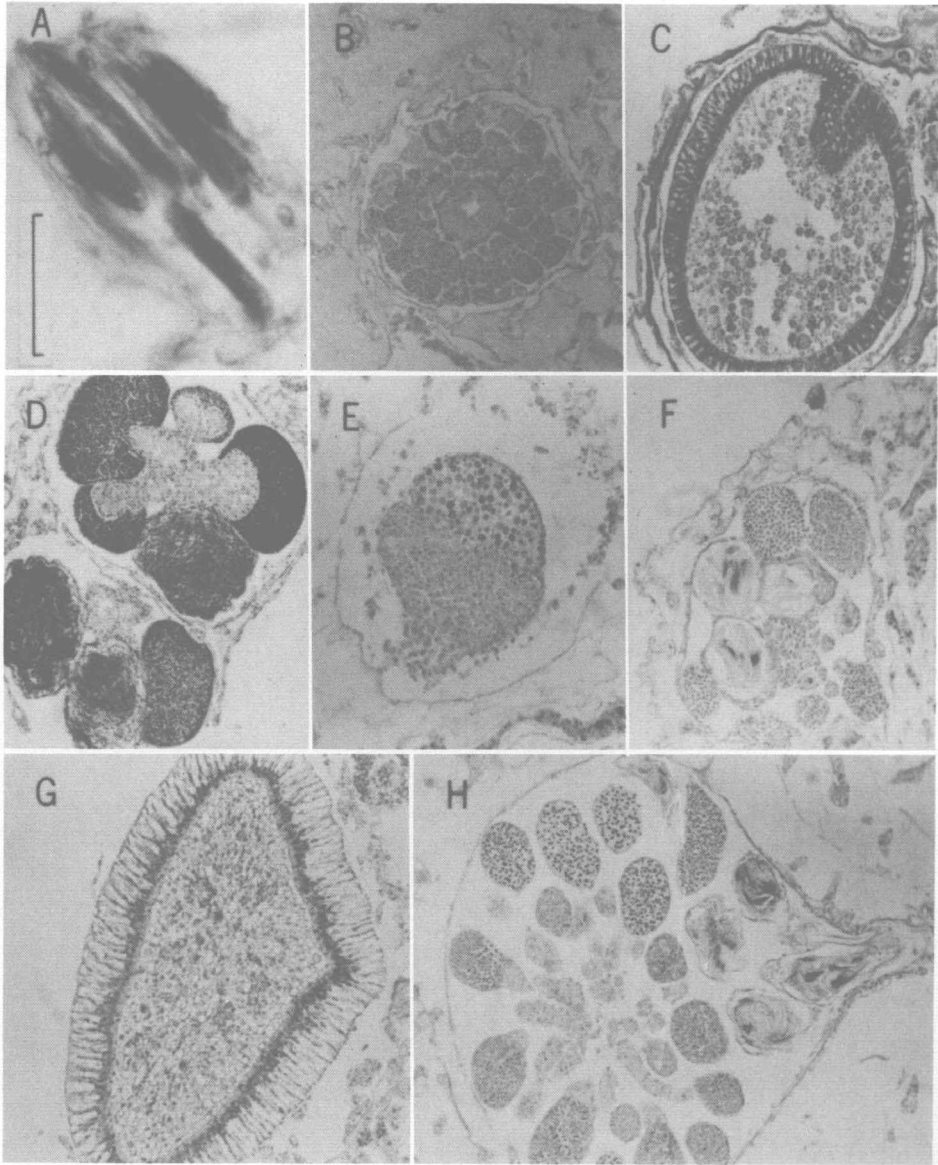


Figure 26. Histological sections of nematocysts and gonophores: A, *Conopora verrucosa*, Edisto 14-2: 71°50'S, 15°50'W, 1,006–1,189 m, 18 Jan. 1959, coenosteal nematophore; B, *Paraerrina decipiens*, syntype, cross section of male gonophore; C, *Distichopora violacea*, Rigili Island, Eniwetok Atoll, cross section of developing female planula; D, *Stylaster roseus*, Carrie Bow Cay, cross section of male gonophores; E, *Stenohelia profunda*, Johnson-Smithsonian Deep-Sea Expt. station 43: 18°04'N, 67°48'W, 439–549 m, 11 Feb. 1933, cross section of egg partially enveloped by spadix; F, *Cryphelia* sp., Albatross-2818: 0°29'S, 89°55'W, 717 m, 15 Apr. 1888, cross section of male gonophores in lid of cyclosystem, nematophore in upper right; G, *Errina antarctica*, Hero 715–874: 54°39'S, 63°50'W, 135–137 m, 26 Oct. 1971, cross section of planula; H, *Conopora verrucosa*, Edisto 14-2: 71°50'S, 15°50'W, 1,006–1,189 m, 18 Jan. 1959, cross section of male gonophores, efferent canal containing mature sperm on right. Scale bar for A = 20 μ m; B–H = 200 μ m.

Diagnosis.—Colonies flabellate, up to 6 cm tall and 8 cm broad. Branches round in cross section and blunt; basal branches up to 5 mm in diameter. Coenosteum covered by shallow pits that are equally spaced about 0.21 mm apart, perhaps the preservation of coenosteal pores of a reticulate texture. Cyclosystems triangular or elongate, the greater axis of the latter parallel to the branch. Elongate cyclosystems about 0.7 mm long and 0.3 mm wide. One of the syntypes has cyclosystems arranged in three longitudinal rows. Dactylopores difficult to detect in the cyclosystems, but according to Nielsen (1919) they are few in number and irregularly scattered around the gastropore. No gastro- or dactylostyles. Craters of ruptured ampullae up to 1.34 mm in diameter.

Discussion.—Boschma (1968a: 100) defined *Congregopora* as “an *Allopore* without gastrostyles,” and another time (Boschma, 1951) implied that its closest affinity was to *Conopora*, differing from this genus primarily by its lesser number of dactylopores per cyclosystem. This is a good guess, but the preservation of the very few Paleocene specimens is not adequate to intelligently discuss its phylogeny, or even to adequately define the genus.

Occurrence.—Paleocene: Denmark (Danian of Fakse).

Type Species.—*C. nasiformis* Nielsen, 1919, by monotypy.

Congregopora nasiformis Nielsen, 1919

Figure 23D–F

Congregopora nasiformis Nielsen, 1919: 21–22, pl. 2, figs. 24–27, text-figs. 3, 10.—Boschma, 1951: 40–42, text-fig. 6a–b; 1956: F100, text-figs. 82, 4a–c; 1957: 40.

Diagnosis.—See that of genus.

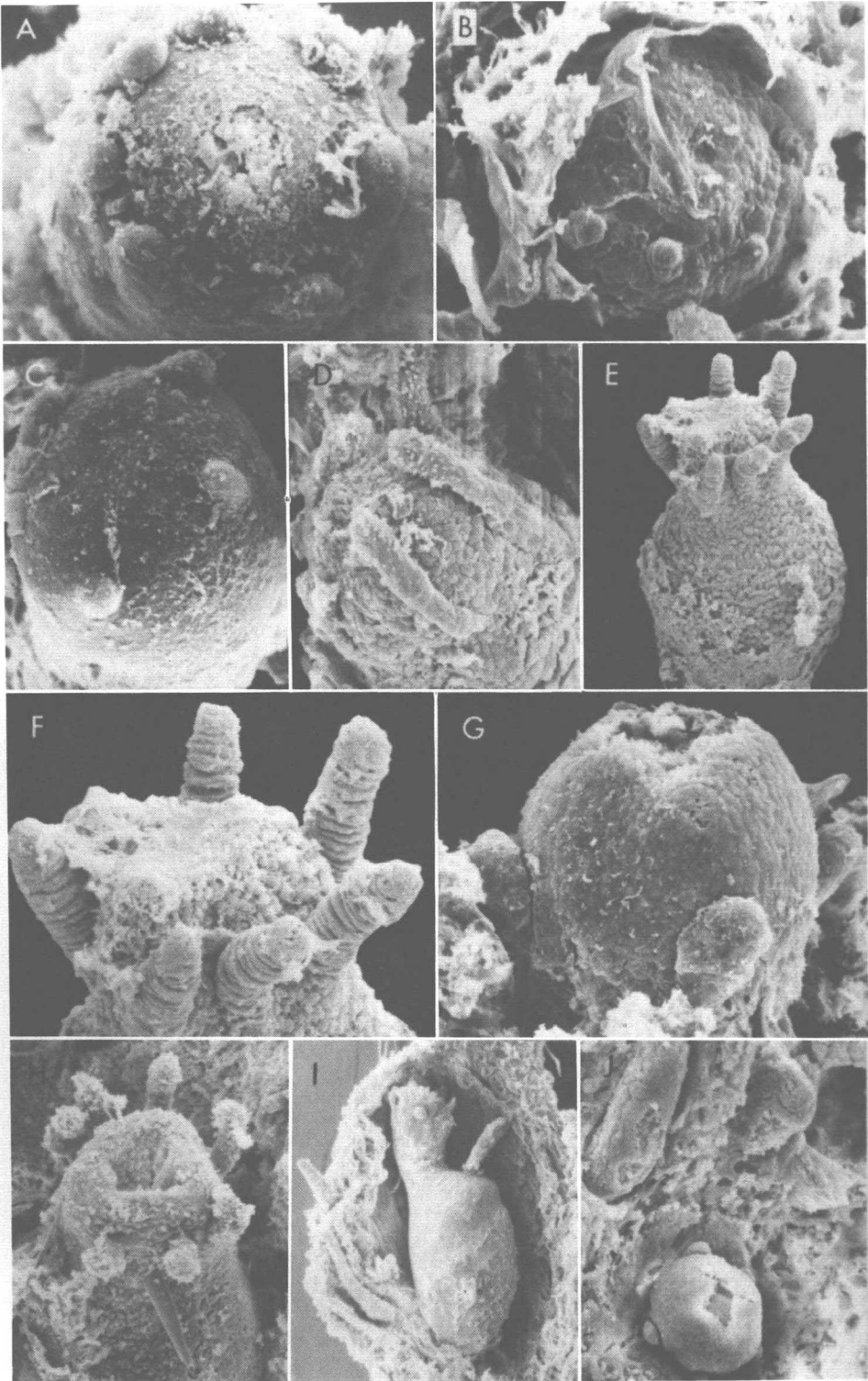
Discussion.—*Congregopora* is a monotypic genus; its single species has been reported only once.

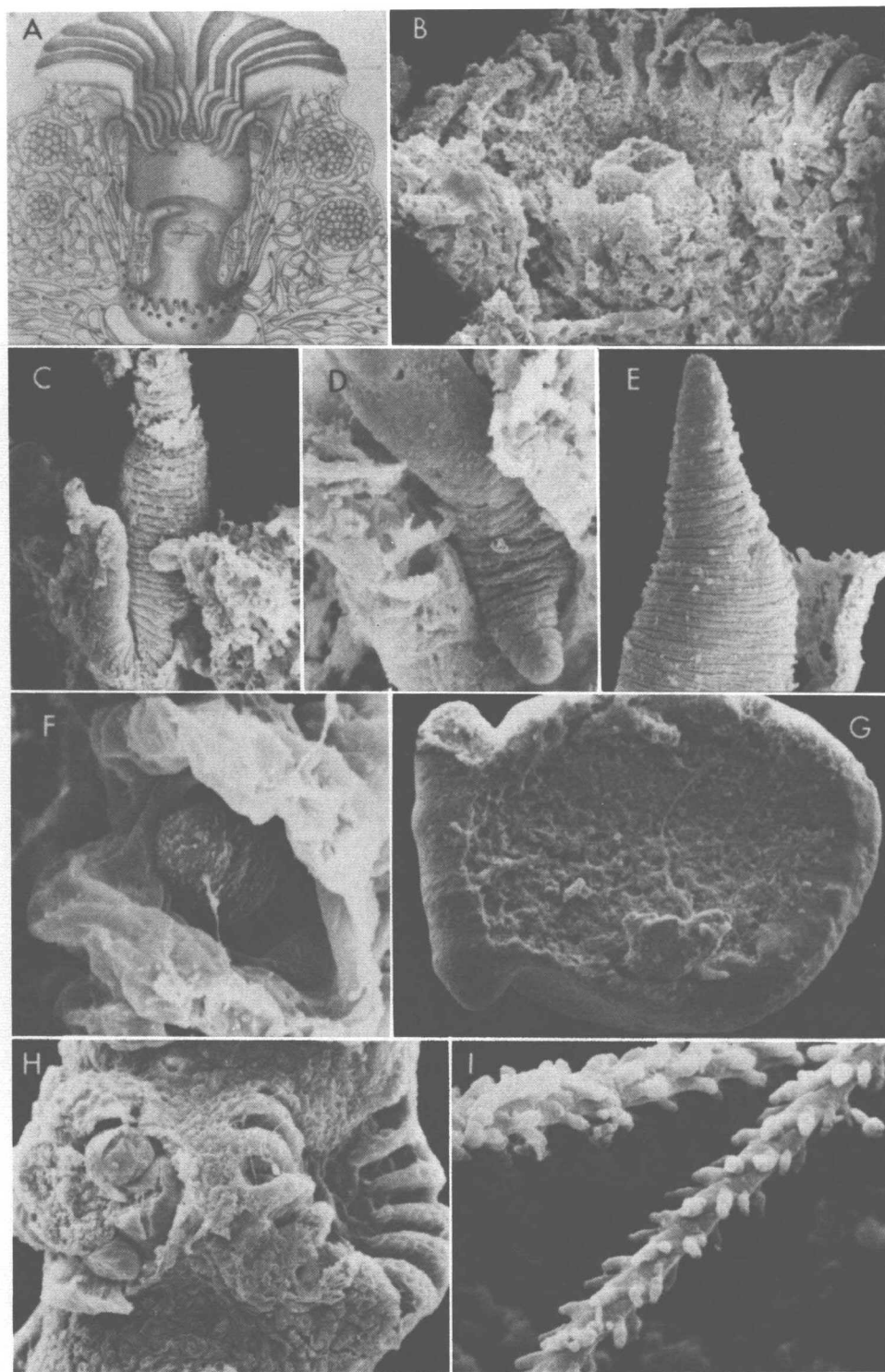
Distribution.—Known only from the Paleocene of Denmark.

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Figure 27. SEM of decalcified, critical-point-dried specimens: A, *Sporadopora dichotoma*, Islas Orcadas 575–82: 55°29'S, 35°20'W, 413–462 m, 6 June 1975, gastrozoid, $\times 143$; B, *Pliobothrus symmetricus*, SABB, BLM-2H: 32°20'N, 78°10'W, 411 m, 15 Feb. 1977, gastrozoid, $\times 160$; C, *Errinopsis reticulum*, Hero 715–879: 54°50'S, 63°50'W, 342–353 m, 28 Oct. 1971, gastrozoid, $\times 215$; D, *Distichopora violacea*, off Rigili Island, Eniwetok, gastrozoid, $\times 270$; E–F, *Stenohelia profunda*, Johnson-Smithsonian Deep-Sea Expedition sta. 43: 18°04'N, 67°48'W, 439–549 m, 11 Feb. 1933, gastrozoid, $\times 107$, $\times 250$, respectively; G, J, *Stylantheca porphyra*, Carmel Bay, California, gastrozoid and gastrozoid with two dactylozooids, $\times 192$, $\times 71$, respectively; H–I, *Adelopora pseudothyron* (H, Eltanin 25–326: 46°04'S, 83°55'W, 298 m, 9 Oct. 1966; I, Eltanin-1521: 54°09'S, 52°08'W, 419–483 m, 30 Jan. 1966); H, gastrozoid, $\times 143$; I, gastrozoid and dactylozooids, $\times 50$.

Figure 28. SEM of decalcified, critical-point-dried specimens: A, Schematic longitudinal section through a cyclosystem and ampullae of *Astyria subviridis* from Moseley (1881: pl. 8, fig. 1), $\times 18$; B, *Cryptothelia* sp., Albatross-2818: 0°29'S, 89°55'W, 717 m, 15 Apr. 1888, longitudinal section through cyclosystem, $\times 66$; C, *Sporadopora dichotoma*, Islas Orcadas 575–82: 55°29'S, 35°20'W, 413–462 m, 6 June 1975, adnate dactylozoid, $\times 57$; D, *Errinopora pourtalesii*, Albatross-3159: 37°47'N, 123°10'W, 49 m, 22 Mar. 1890, adnate dactylozoid, $\times 150$; E, *D. (Haplomerismos) anceps*, paratype, tip of dactylozoid, $\times 180$; F, *Stylaster roseus*, Carrie Bow Cay, Belize, tip of dactylozoid between two pseudosepta, $\times 420$; G, *Adelopora pseudothyron*, Eltanin-1521: 54°09'S, 52°08'W, 419–483 m, 30 Jan. 1966, underside of undecalcified operculum showing retractor muscle, $\times 107$; H, *Stylaster roseus*, Carrie Bow Cay, Belize, cyclosystem and damaged male ampulla, $\times 54$; I, *Inferiolabiata labiata*, Eltanin-1536: 54°29'S, 39°22'W, 659–686 m, 8 Feb. 1966, shafts of exploded nematocysts, $\times 8,450$.





Types.—Deposited at the Geologisk Museum, Copenhagen. Examined by the author.

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NOTE: The paper referred to as Cairns, In press, on Antarctic Stylasterina should be published before this paper, as intended; however, because it was only in galley stage when this paper was written, complete citations are not given here.